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THE IDENTITY OF *RHYTIDEA BICOLOR* LINDL., A GEOPHYTE COLLECTED IN CALIFORNIA BY WILLIAM LOBB

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ABSTRACT

In 1856 John Lindley made the first description of the firecracker flower, *Rhytidea bicolor* (now known as *Dichelostemma ida-maia*), naming a William Lobb collection exhibited in London. This binomial, despite its obvious priority, was proposed to be relegated to synonymy in Taxon, and is discussed here further.

RESUMEN

En 1856 John Lindley hizo la primera descripción de la flor *firecracker*, *Rhytidea bicolor* (ahora conocida como *Dichelostemma ida-maia*), nombrando una colección de William Lobb exhibido en Londres. Este binomial, a pesar de su prioridad, fue propuesto para ser relegado a la sinonimia en Taxón, y se discute aquí más.

Key Words: *Dichelostemma*, Gardeners' Chronicle, Lindley, Lobb, principle of priority, *Rhytidea*, Veitch.

In the nineteenth century, the British nursery firm of Veitch sent out plant-collectors to many parts of the world (Veitch 1906, Heriz-Smith 1988, 1989). William Lobb (1809–1864) collected in South America (1840–1848), and in California and Oregon (1849–1857) (Ewan 1973). In preparation for a new edition of *Mabberley's Plant-book* (Mabberley 2008), I found it necessary to look into Lobb's introductions; one of those was the plant now known as *Dichelostemma ida-maia* (Alph. Wood) Greene (Hoover 1940).

RHYTIDEA BICOLOR

In 1856, "a new hardy bulb from California" was introduced by Veitch at the Crystal Palace likely from collections made by Lobb (Gardeners' Chronicle, p. 375), and later that same year published by Lindley as *Rhytidea bicolor* Lind. (1856, p. 420). The description is unmistakably the firecracker flower, now known as *Dichelostemma ida-maia* (Alph. Wood) Greene (Asparagaceae: Brodiaeoideae). Lobb collected for Veitch in California in 1849–51, there and in Oregon in 1852, returning again to California from 1854–1857 (Veitch 1906, Ewan 1973). Lobb stayed in California after ending his contract with Veitch, and died in San Francisco (Veitch 1906).

Dichelostemma ida-maia is based on *Brevoortia ida-maia* Alph. Wood, published over a decade later (Wood 1867). How Lindley's generic name came to be overlooked is unknown. It seems likely that the first introduction of the firecracker flower was not successful in cultivation; the plant was not listed in the Veitch catalog (1906). A collection from Bolander was grown at Kew and Ipswich, and so Hooker introduced *Brevoortia coccinea* (A. Gray) S. Watson (a synonym) to England in 1870, noting the initial discovery of the plant by Lobb.

NOMENCLATURE

Rhytidea Lindl. postdates *Dichelostemma* Kunth, so does not pose a threat to the accepted generic name for the firecracker flower. *Rhytidea* would have precedence over *Brevoortia* Alph. Wood, should the plant ever be reconsidered worthy of separate generic status. It is worth noting that *Brevoortia* Gill (1861), also named after James Carson Brevoort (1818–1887), is the currently accepted name of a genus of fish, the menhadens of the Clupeidae.

Making a new combination in *Dichelostemma* based on *Rhytidea bicolor* would disturb almost 150 years of usage of the epithet '*ida-maia*', so such a course of action is not favored here. A formal proposal for rejection of *Rhytidea bicolor* Lindl. was prepared for *Taxon* (2015).

ACKNOWLEDGMENTS

I am greatly indebted to Christine Bartram (CGE) and Anna Trias Blasi (K) for information on specimens in their care. My daughter, Laura (Madrid), arranged for the Spanish translation of the abstract.

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GENETIC STRUCTURE AND DEMOGRAPHY OF *CHLOROPYRON PALMATUM*, AN ENDANGERED ANNUAL PLANT

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ABSTRACT

Chloropyron palmatum (Ferris) Tank & J.M Egger (formerly *Cordylanthus palmatus* [Ferris] J. F. Macbr.) is an annual plant that inhabits seasonally flooded wetlands with saline and alkaline soils in California. In 1986, the plant was listed as endangered under the U.S. Endangered Species Act. We aimed to inform conservation strategies for the species' five remaining populations by examining the genetic diversity and structure of the populations (on the basis of nuclear DNA markers) and their potential response to demographic and environmental stochasticity. We also assessed fluctuations in population size and whether there was evidence of hybridization between *C. palmatum* and *Chloropyron molle* (A. Gray) A. Heller subsp. *hispidum* (Pennell) Tank & J.M. Egger (formerly *Cordylanthus mollis* A. Gray subsp. *hispidus* [Pennell] T.I. Chuang & Heckard). Populations of *C. palmatum* were genetically distinct with a F_{ST} of 0.23, indicating substantial genetic structure among populations. Within populations, there was no evidence of isolation by distance. However, individuals in two adjacent vernal pools were genetically distinct. The pattern of genetic variation within populations suggests that the historical frequency and extent of seed dispersal by overland flooding has strongly affected the genetic structure of populations. Despite founder effects and population bottlenecks, small and large populations had similar levels of genetic variation. We found no evidence of hybridization. All extant populations of *C. palmatum* are genetically variable and distinct. We recommend that hydrologic connectivity be considered if seeds are collected and sowed with the intent of increasing the size of natural populations or creating experimental populations.

Key Words: alkali wetlands, *Cordylanthus palmatus*, genetic structure, hydrological connectivity, inter-simple sequence repeats (ISSRs), palmate-bracted bird's beak, vernal pools.

Declines in occupancy and abundance of most species are caused by habitat loss and reductions in habitat quality (Foin et al. 1998). Often these declines are accompanied by genetic changes, but focusing on genetics as a means to maintain or restore plant populations is relatively uncommon (Hufford and Mazer 2003). However, when habitat is highly limited and cannot be restored or reconstructed, genetics may be relevant to in situ conservation efforts such as increasing population sizes and establishing seed banks, particularly for annual plants (Ramp et al. 2006). Many plants, especially rare taxa, are associated with certain microhabitats (Maliakal-Witt et al. 2005). When these microhabitats occur in discrete, small patches, the genetics of populations and species may diverge at fine spatial resolution. If genetic data are assessed relative to potential drivers of genetic structure (i.e., the distribution of genetic variation within and among populations), they can inform efforts to maintain or simulate ecological phenomena that affected the microevolution of the species.

Genetic structure develops over ecological and evolutionary time. When gene flow is reduced, populations can diverge in response to the random processes of mutation and drift, directional processes such as natural selection, or both. Conversely, genetic divergence can be forestalled when gene flow is frequent and widespread. By combining data on genetic structure, trends in population size, and breeding system and field observations of potential mechanisms of gene flow, one can identify biotic and abiotic drivers of genetic structure.

Chloropyron palmatum (Ferris) Tank & J.M Egger (Orobanchaceae) is an annual plant that inhabits seasonally flooded wetlands with saline

and alkaline soils in California's Central and Livermore valleys. The plant survives the dry summer through hemiparasitism (Chuang and Heckard 1971), excretion of salt crystals through its leaves, and deep rooting (USFWS 1998). The species was listed as endangered under the California and United States Endangered Species Acts in 1984 and 1986, respectively, due to the small sizes of or threats to the five remaining populations. Geographic distances among populations exceed the probable dispersal ability of the species, and virtually no other habitat remains. Accordingly, understanding of genetic structure may be a substantial asset to planning and implementation of in situ and ex situ conservation actions for the species.

Experiments in which enclosed flowers on individual plants were hand pollinated with pollen from the same plant suggested that *C. palmatum* is self-compatible (CCB 1993 unpublished data). *Chloropyron palmatum* is believed to be insect pollinated because the flowers are closed at anthesis, and therefore wind pollination is unlikely (Iwanami et al. 1988). Experiments demonstrated that neither fruit nor seed set in the absence of pollinators (CCB 1993 unpublished data). A few studies found that *Bombus californicus* Smith, 1854 and *B. vosnesenskii* Radoszkowski, 1862 pollinate *C. palmatum* (CCB 1994, Lee and Associates 2002). However, *C. palmatum*, like other plants with relatively long flowering periods, may have a succession of pollinators. In addition to *Bombus*, these pollinators appear to include solitary bees, such as *Halictus* spp. Latreille, 1804 and *Lasioglossum* spp. Curtis, 1833 (CCB 1992, Lee and Associates 2002). Scanning electron micrographs of the legs of halictid bees collected at flowers of *C. palmatum* confirmed that the bees could carry *C. palmatum* pollen (CCB 1992). Nonetheless, the low fruiting rate of plants from which *Bombus*, but not *Halictus*, experimentally were excluded suggested that the small, solitary bees did not play a substantial role in pollination (CCB 1994).

In general, bees begin to collect pollen at the lowest flower of a columnar inflorescence, such as the spike in *C. palmatum*, and move upward (Proctor and Yeo 1972). Bees then fly to inflorescences on neighboring plants, with occasional longer-distance flights. Previous observations suggested that *B. californicus* transports considerable amounts of *C. palmatum* pollen within and among plants, potentially facilitating both inbreeding and outcrossing (CCB 1993 unpublished data, CCB 1994). Further work suggested that that *Bombus* remain in a given patch of *C. palmatum* during the period in which they are foraging on that species (CCB 1994). A potential consequence of this behavior is limited transfer of pollen among patches of *C. palmatum*. If seed dispersal is limited, then the net result of self-compatibility and limited pollen movement is development of genetic structure at a resolution commensurate with pollination distance.

The small size, crested coats, and hair-like wax extrusions of *C. palmatum* seeds (Chuang and Heckard 1972) suggest that they are dispersed by water (Howe and Smallwood 1982). A laboratory study showed that fresh seed could float well for six days (Ayres unpublished data). However, earlier field and greenhouse studies suggested that *C. palmatum* seeds also are dispersed by gravity (CCB 1993 unpublished data, CCB 1994). Because *C. palmatum* occurs in areas with anthropogenic impediments to the flow of surface water, we aimed to determine whether genetic structure within populations could be attributed to hydrologic isolation. Long-distance dispersal of buoyant seeds by surface water might prevent development of genetic structure within populations, whereas restricted surface-water movement or dispersal of seeds by gravity might lead to fine-resolution genetic structure. Patches of wetlands inhabited by *C. palmatum* include alkali or saline vernal pools of several hundred square meters and an alkali sink with dozens of connected and isolated vernal pools and swales.

A previous genetic study of *C. palmatum* based on six polymorphic enzyme loci found that approximately 98% of genetic variation was contained within populations, whereas 2% of genetic variation occurred among populations (Fleishman et al. 2001). One of the five populations contained a disproportionate amount of the within-population genetic variability (Fleishman et al. 2001). Fine-grained genetic structure (less than four meters) was detected in the latter population. Because lack of isozyme polymorphism may have affected those inferences, we used many nuclear DNA loci to investigate genetic structure. *Chloropyron molle* A. Gray subsp. *hispidum* (Pennell) Tank & J.M. Egger is sympatric with the most genetically variable population of *C. palmatum*. Therefore, we also aimed to determine whether hybridization between the two species might explain increased enzyme allelic diversity in this population. The ultimate goal of our research was to inform conservation strategies for *C. palmatum* by increasing our understanding of microevolutionary processes (Ayres et al. 2007).

Methods

Study System

We examined genetic variation and estimated abundance of all five known populations of *C. palmatum*. Climate throughout the species' range is similar. Virtually all precipitation occurs as rain during the winter, and summers are hot

and dry. *Chloropyron palmatum* grows on seasonally flooded, saline-alkali soils in lowland plains and basins. It grows primarily along the edges of channels and drainages, with a few individuals scattered in seasonally wet depressions, alkali scalds, and grassy areas. *Chloropyron palmatum* occurs with other species tolerant of high salt concentrations, such as iodine bush (*Allenrolfea occidentalis* [S. Watson] Kuntze), alkali heath (*Frankenia salina* [Molina] I.M. Johnst.), glasswort (*Arthrocnemum subterminale* [Parish] Standl.), bush seepweed (*Suaeda nigra* J.F. Macbr.), and salt grass (*Distichlis spicata* [L.]).

The Mendota population (Fresno County) is the southernmost population of *C. palmatum*. It occurs within the Alkali Sink Ecological Reserve, which covers approximately 380 ha. Within the reserve, *C. palmatum* is associated with iodine bush and other native shrubs. Host plants have not been identified conclusively, but in 1988 most *C. palmatum* grew within 2 m of bush seepweed (*Suaeda nigra*) and rusty molly (*Kochia californica* S. Watson) (E. Cypher, unpublished data).

The Livermore population (Alameda County) is located in the southern part of a ca. 7000 ha hydrologic basin, the Springtown Alkali Sink. About 300 ha of the sink, of which 109 ha are owned by the city of Livermore and designated as a preserve, are a mosaic of alkali sink shrubs and grasses, annual grasslands dominated by non-native species, natural and channelized stream drainages, and permanent and seasonal streams and vernal pools. The upper portions of the basin contain agricultural lands and annual grasslands.

The Woodland population (Yolo County) occurs on the 73 ha Alkali Grasslands Preserve, which is owned by the city of Woodland and a private citizen. The preserve is dominated by annual grasses with areas of alkali grasses, seasonal pools and swales, a vernal lake, irrigation channels, and levees. The most abundant annual grasses are non-native species, especially *Lolium perenne* L. subsp. *multiflorum* (Lam.) Husnot. The hydrology of the preserve has been highly altered by agricultural activities. In at least two years (1974 and 1984), no mature plants or seedlings of *C. palmatum* were observed (M.A. Showers, personal observations); the population likely reestablished from the soil seed bank. Within the preserve, *C. palmatum* occurs in two locations separated by ca. 1.6 km but connected by seasonal drainages.

The Colusa population (Colusa County) is located within the 1,872 ha Colusa National Wildlife Refuge. Colusa National Wildlife Refuge lies within the Colusa Basin and historically was covered by alkali vernal pools and associated alkali meadows. Prior to its designation as a refuge, the land was used for livestock grazing and for growth of winter wheat and rice. Parts of the refuge subsequently have reformed into functional vernal pools and alkali meadows. We sampled *C. palmatum* from two adjacent vernal pools.

The Delevan National Wildlife Refuge (Colusa County) includes more than 1820 ha of intensively managed wetlands and 486 ha of uplands. *Chloropyron palmatum* occurs primarily in alkali meadows and large vernal pools, with plants scattered along the roadsides.

Demographic Assessments

In 1992, monitoring methods were developed to rapidly assess the distribution and abundance of *C. palmatum* (CCB 1992). Initially validated on the Livermore population, these methods were sufficient to identify substantial changes in abundance relatively cheaply and quickly. In brief, transects that collectively represented local gradients in land cover and habitat quality were established in four subareas of the site. Each transect was subdivided further into segments representing different vegetation types that were known to support *C. palmatum* or that appeared to be habitat for the species. Observers walked along each transect segment for a predetermined period of time. The number of *C. palmatum* was estimated on a semi-logarithmic scale (none, tens to hundreds, thousands to tens of thousands, and so forth). The number of individuals in each subarea was estimated by summing the totals for each segment.

In 1992 and 1993, populations of *C. palmatum* were surveyed at the Delevan and Colusa National Wildlife Refuges and the Mendota Alkali Sink Ecological Reserve (CCB 1993 unpublished data, CCB 1994). The Woodland population was surveyed in 1992 (CCB 1993 unpublished data). We visited all populations in 2004, and land managers again visited each population in 2012 or 2013. During each visit, biologists familiar with the species estimated population sizes within an order of magnitude on the basis of the rapid-assessment method described above. In addition, refuge managers have conducted annual censuses of the populations at the Delevan and Colusa National Wildlife Refuges since 1997 (J. Silviera unpublished data) and local biologists have conducted annual censuses of the Livermore, Mendota, and Woodland populations (S. Bainbridge unpublished data, E. Cypher unpublished data, C. Little unpublished data).

Genetic Analyses

We sampled 30–35 plants in each of the five extant populations of *C. palmatum* from April to June 2004. We collected two to three short (<5 cm), robust, green branches per plant. The coordinates of each sampled plant were recorded

with a Geoexplorer 3 global positioning system (GPS) meter (Trimble, Sunnyvale, CA). At the Springtown Alkali Sink, we took six samples from a population of *C. molle* subsp. *hispidum* that co-occurred with *C. palmatum* to develop species-specific DNA fragments that could be used to test whether the species hybridize.

We extracted DNA with the proteinase K method detailed in Daehler et al. (1999) at UC Davis. Our preliminary screening of primers identified 28 inter-simple sequence repeat (ISSR) primers (of 100 examined; Nucleic Acid Protein Service Unit Kit #9, University of British Columbia, Vancouver, Canada; http://naps.msl.ubc.ca) that amplified *C. palmatum* or *C. molle* subsp. *hispidum* DNA fragments. These are dominant markers that are scored as present or absent. We did not include samples from the Livermore population of *C. palmatum* in the preliminary screening. Instead, we wished to identify species-specific bands for *C. palmatum* from allopatric populations to investigate potential hybridization. We used an Eppendorf Mastercycler Gradient thermalcycler to simultaneously optimize $MgCl_2$ and annealing temperature; 17 and 12 primers had annealing temperatures of 50°C and 54°C, respectively. We also screened RAPD (Random Amplified Polymorphic DNA) primers obtained originally from Operon Technology (now known as Qiagen Operon, Inc., Alameda, CA); primers and temperatures are in Appendix 1 (ISSR) and Appendix 2 (RAPD).

We used a final set of 118 bands for our genetic analyses: 86 ISSR bands were polymorphic in *C. palmatum* (69 of these bands were absent in *C. molle* subsp. *hispidum*), 25 ISSR bands were specific to and ubiquitous in *C. molle* subsp. *hispidum*, and 7 bands were specific and ubiquitous in *C. palmatum*. The RAPDs primers were successful for an average of 82% of the samples; as our cut-off value was 90%, they were not used in any further analyses. We used individuals that were scorable for 90% of the DNA bands: 32 individuals of *C. palmatum* from Colusa, 28 from Delevan, 28 from Livermore, 29 from Mendota, and 25 from Woodland (total scored = 142), and 6 individuals of *C. molle* subsp. *hispidum* that were collected from the Livermore site.

PCR conditions were 94°C for 90 sec followed by 40 cycles of 94°C for 15 sec, the optimized annealing temperature for 30 sec, and 72°C for 2 min. Reaction volumes of 15 mL contained, by volume, 10% $MgCl_2$-free 10X reaction buffer A (Promega, Madison, WI), 0.6 units Taq polymerase (Promega, Madison, WI), 360 picounits primer (University of British Columbia, Vancouver, Canada), 3 mmol/L $MgCl_2$, 200 mmol/L each of dATP, dCTP, dGTP, and dTTP (Promega, Madison, WI), and 30 ng genomic DNA. We repeated most reactions to confirm consistency. Following electrophoresis on 1.5% agarose gels, we stained DNA with ethidium bromide and visualized the DNA under ultraviolet light. We hand-scored polymorphic DNA fragments in the gels.

Data Analyses

We calculated genetic distance between individuals with a Euclidean distance metric implemented with NTSTSpc (version 2.10 Exeter Software, Setauket, NY). We visualized hierarchical patterns of genetic distance with the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering method applied to Sequential, Agglomerative, Hierarchical, and Nested (SAHN) cluster analysis. We calculated the geographic distance between individual *C. palmatum*. We calculated and tested the correlation between genetic and geographic distance among and within populations with 1000 permutations of a Mantel test (Mantel 1967). We conducted Mantel tests with the Matrix Comparison Plot program of NTSYS.

We used the program Arlequin 3.0 (Excoffier et al. 1992; http://lgb.unige.ch/arlequin/) to calculate a matrix of squared Euclidean genetic distances between all individuals. We included 79 loci (of 86) in the analysis after removing loci with replicate patterns or with >5% missing values. We then partitioned the matrix into submatrices corresponding to subdivisions identified by the UPGMA cluster analysis. The sums of squares in the matrix and submatrices yield sums of squares for the hypothetical divisions in the population. We included the sums of squares in an analysis of molecular variance (AMOVA), which allowed us to test simultaneously whether genetic distances varied between and within groups.

We analyzed both regional genetic structure and genetic differences between *C. palmatum* in two vernal pools within the Colusa National Wildlife Refuge (see above). We calculated a matrix of pairwise differences among populations with Arlequin 3.0. We then applied UPGMA and SAHN cluster analysis to generate a population-level dendrogram of genetic relatedness.

We counted the number of the 86 ISSR polymorphic loci that were variable within each population of *C. palmatum*.

Results

Demographic Assessments

The Mendota Alkali Sink Ecological Reserve contained 800 *C. palmatum* in 1987, but no seedlings or adult plants were observed in the early 1990s. In 2013, 3000 plants were observed (Fig. 1, E. Cypher, unpublished data); presumably these plants germinated from the soil seed

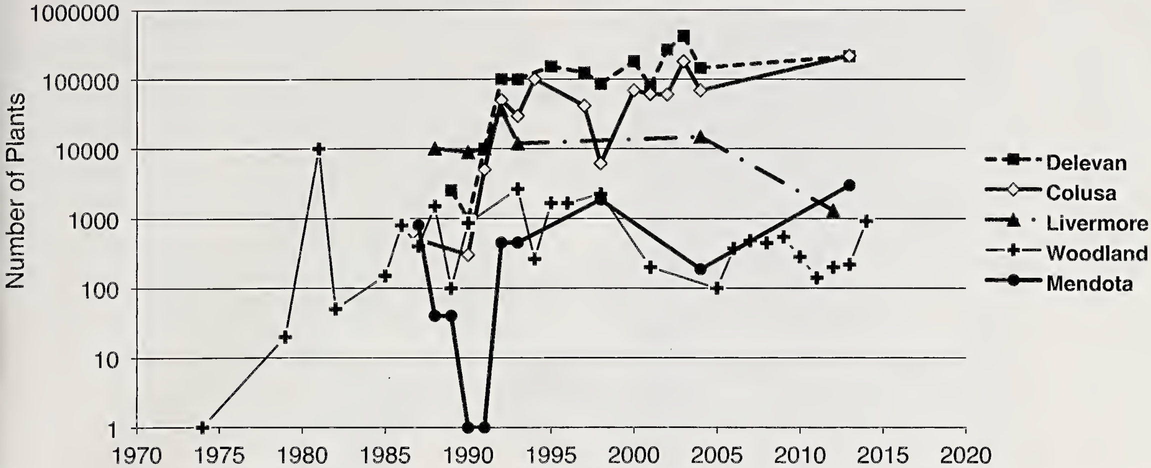

FIG. 1. Changes in abundance of *Chloropyron palmatum* within the five extant populations; note the y-axis is log scale.

bank. Similarly, the Woodland population was nearly extirpated in the mid 1970s. The size of the Woodland population increased to 5000 in 1982, crashed again in the mid 1980s, and has not exceeded a few hundred plants since (Fig. 1, M. Showers and C. Little, unpublished data).

Until recently, annual abundances of *C. palmatum* in the Colusa, Delevan, and Livermore populations ranged from several hundred to many thousands. Since the early 1990s, the number of *C. palmatum* in the Colusa population has fluctuated 3-fold to 7-fold annually; in 2013, more than 200,000 plants were observed at both Colusa and Delevan National Wildlife Refuges (J. Silviera unpublished data, J. Isola unpublished data). For about two decades, the Livermore population was the most stable, with approximately 10,000 individuals, but in 2012 the abundance of *C. palmatum* decreased to 1,100. Multiple factors have been hypothesized to reduce habitat quality at the Springtown Alkali Sink, including altered hydrology, use of off-road vehicles, and invasion by perennial pepperweed (*Lepidium latifolium* L.) and non-native grasses (S. Bainbridge, personal communication).

Genetics

We found no evidence of hybridization between *C. palmatum* and *Chloropyron molle* subsp. *hispidum*. We detected none of the 25 bands specific and ubiquitous to *C. molle* subsp. *hispidum* in the Livermore population or in any other population of *C. palmatum*. We did not detect any of the 76 bands specific to *C. palmatum* in *C. molle* subsp. *hispidum*.

Multivariate cluster analysis of genetic similarity between individual *C. palmatum* indicated that the Mendota population was genetically distinct from the four populations to the north (Fig. 2). Individuals from the Delevan and Livermore populations were genetically similar within populations and distinct between populations, whereas the Colusa and Woodland populations were less distinct. In addition to the small, labeled Mendota and Delevan clusters (Fig. 2), 14 individuals were placed in different population clusters than their origin, most especially the individuals collected at Delevan and Mendota. Within populations, we found no correlation between genetic and geographic distance among individuals.

We found no genetic structure between the putative Woodland subpopulations. However, individuals from each vernal pool at Colusa grouped together. In addition, six samples taken from a small roadside aggregation of plants (<20 individuals) at the Delevan National Wildlife Refuge, separated by only 14 linear m from individuals growing in a vernal pool, were genetically distinct from other *C. palmatum* at Delevan (Fig. 2).

On the basis of the hierarchical genetic patterns revealed by multivariate cluster analysis, we

TABLE 1. ANALYSES OF MOLECULAR VARIANCE (AMOVA) AMONG AND WITHIN POPULATIONS OF *CHLOROPYRON PALMATUM*. Potential genetic structure within the Colusa population not included.

Source of variation	df	Sum of squares	Variance	% of variation (P-value)	F_{ST}
Among populations	4	315.74	2.38	22.0 (<0.001)	
Within populations	143	1208.3	8.45	78.0 (<0.001)	
					0.22 (<0.001)

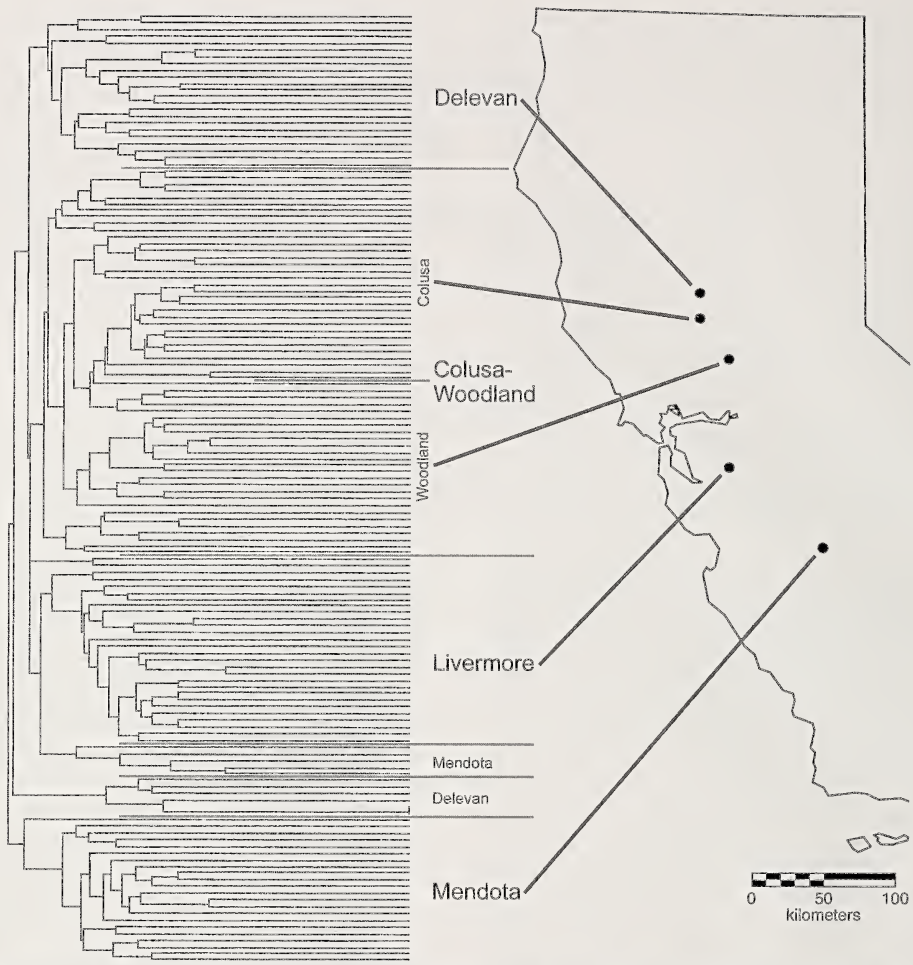

FIG. 2. Individual *Chloropyron palmatum* clustered on the basis of genetic similarity and the location of populations within California, USA.

performed two AMOVA. The first AMOVA did not account for potential differences among putative subpopulations (Table 1), whereas the second AMOVA incorporated potential differences between individuals from two vernal pools at Colusa National Wildlife Refuge (Table 2). In both analyses, 76–78% of genetic variation occurred within populations and the remaining genetic variation occurred among populations or subpopulations, resulting in similar F_{ST} values of ca. 0.22 ($P < 0.001$). In the second analysis, almost 10% of among-population variation was attributed to subpopulation structure at Colusa.

Cluster analysis of pairwise differences between populations indicated division between northern and southern populations (Fig. 3). The dendrogram based on genetic similarity among individuals suggested that the Livermore population was more closely related to the northern than the southern populations. However, the population-level analysis suggested that the Livermore population was most closely related

TABLE 2. ANALYSES OF MOLECULAR VARIANCE (AMOVA) AMONG AND WITHIN POPULATIONS OF *CHLOROPYRON PALMATUM*. Potential genetic structure within the Colusa population included.

Source of variation	df	Sum of squares	Variance	% of variation (P-value)	F_{ST}
Among populations	4	315.74	1.44	13.28 (0.067)	
Among putative subpopulations	1	25.9	1.06	9.84 (<0.001)	
Within populations	143	1182	8.33	76.89 (<0.001)	
					0.23 (<0.001)

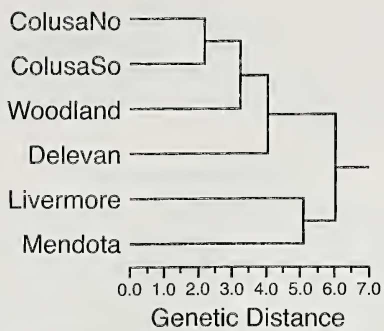

FIG. 3. Populations of *Chloropyron palmatum* clustered on the basis of genetic similarity; ColusaNo and ColusaSo are two adjacent vernal pools separated by 120 m.

to, although genetically distant from, the southernmost population, Mendota. The genetic structure of the northern population group generated by the population-level analysis was consistent with that from the individual-based dendrogram.

Populations of *C. palmatum* contained an average of 59 ± 3 (mean ± SD) of the species' 86 polymorphic loci (Mendota and Livermore, 56; Colusa, 58; Delevan, 61; Woodland, 63).

DISCUSSION

Conservation efforts generally aim to maintain not only distribution and abundance of a given species but its evolutionary potential (Hufford and Mazer 2004). Conservation of evolutionary potential requires both an assessment of genetic structure and an evaluation of potential mechanisms that create genetic structure. We employed neutral genetic markers to assess gene flow and genetic variation in *C. palmatum* and evaluated the mechanisms by which gene flow might occur. However, we did not assess genetic structure that may reflect environmental adaptation.

Gene flow in plants occurs either by movement of haploid gametes in pollen grains or by seed dispersal. We found that geographic and genetic definitions of populations of *C. palmatum* were similar, suggesting that populations have been isolated for many generations. Historically, thousands of acres of the Colusa Basin from Knight's Landing to Willows were alkali flats, vernal lakes and pools that were eventually converted to rice acreage (Silviera 2000), fragmenting what may have been a vast ancestral population of *C. palmatum*, to the current isolated remnant populations at Delevan, Colusa, and Woodland. This would explain their close genetic affinities, especially between the Colusa and Woodland populations (Fig. 2). It is likely that the Livermore population, hemmed in by hills, and the Mendota population, 290 km distant from Woodland were always isolated. There was no apparent genetic structure within the Mendota, Livermore, and Woodland populations. In contrast, individuals in two adjacent vernal pools at Colusa were genetically distinct. Although we did not detect structure within the Delevan population, our sample sizes from several vernal pools were insufficient to be confident that no genetic differences exist. Genetic structure at the level of vernal pools has been considered as a theoretical possibility (e.g., Elam 1998). Recently, Gordon et al (2012), using microsatellites, found genetic structure among vernal pools within locations in *Neostapfia colusana* (Burtt Davy) Burtt Davy (F_{ST} = 2.73) and *Tuctoria greenei* (Vasey) Reeder (F_{ST} = 7.4).

Early genetic analyses of species that inhabit vernal pools examined species-level genetic structure based on isozyme variation (Crawford and Ornduff 1989, Dole and Sun 1992). A challenge in basing genetic inferences on isozymes, especially for rare species, is that the enzymes are not sufficiently variable to allow robust analysis of population structure. For example, six of nine putative populations of *Limnanthes floccosa* Howell subsp. *californica* Arroyo were invariant at 28 isozyme loci, and variable populations were polymorphic at but a single locus (Dole and Sun 1992). By contrast, a DNA-based study of these populations found that over 50% of 457 plants had unique genetic profiles, and identified 20 genetically distinct populations (Sloop et al. 2011).

Previous genetic analyses of *C. palmatum* that were based on isozyme alleles (Fleishman et al. 2001) yielded an F_{ST} of 0.019, less than 10% of the genetic structure we detected with nuclear DNA markers. In addition, previous work suggested that the large populations at Delevan and Colusa National Wildlife Refuges were virtually invariant, whereas we found that almost 60% of ISSR loci within these populations were variable. However, our estimate of total variation was affected by our use of polymorphic DNA markers. Both the allozyme and the DNA analyses found that genetic variability was not correlated with population size. We believe that the isozyme analysis did not contain enough alleles to discriminate adequately among genotypes and therefore underestimated genetic divergence.

It appears that relatively small populations of *C. palmatum*, even those with a history of severe bottlenecks, can contain relatively high levels of genetic variation. Past differences in abundance between the Mendota and Livermore populations notwithstanding, the number of polymorphic loci in the two populations was the same. Despite two recent population bottlenecks, the small Woodland population contained the greatest number of polymorphic loci, comparable to the much larger population at Delevan. Maintenance of genetically variable populations regardless of

demographic stochasticity is likely attributable to a genetically variable soil seed bank. In the endangered vernal pool endemic *Limnanthes vinculans* Ornduff, temporal genetic structure within a given vernal pool varied substantially among years, indicating that single-year estimates may not reflect the genetic variation retained in the soil seed bank (Sloop et al. 2012).

Our results suggest that hydrologic connectivity may have a considerable effect on genetic structure within populations and that dispersal of buoyant seeds has facilitated long-term gene flow in *C. palmatum*. For example, lack of genetic structure within the Livermore and Woodland populations may reflect historical or recent overland flow. By contrast, genetic differences between individuals in adjacent vernal pools at the Colusa National Wildlife Refuge suggest that overland flow between the pools is infrequent.

Application of Results to Conservation

Our work suggests that conservation efforts for *C. palmatum* are most likely to be effective when historical patterns of hydrology are maintained. We suggest maintaining both hydrologic barriers in populations with genetic substructure and overland flow in populations without local genetic substructure.

If historical patterns of overland water flow cannot be maintained, then mixing of seed collected from throughout a given population may mimic historical exchange of genes within that population. However, mixing seed may disrupt locally coadapted gene complexes or generate outbreeding depression (Hufford and Mazer 2003, but see Frankham et al. 2010). There is considerable evidence that local adaptation strongly affects genetic structure in plants (Linhart and Grant 1996); in most cases, there appears to be no correlation between neutral genetic markers and morphological traits (McKay and Latta 2002). Accordingly, genetic structure that is driven by gene flow and revealed by selectively neutral molecular markers may not correspond with morphological patterns driven by long-term environmental adaptation. Moreover, mitigation efforts that sow seeds across a relatively large area may lead to genetic homogenization, possibly reducing microevolutionary potential (Halbur et al. 2014).

Because all populations of *C. palmatum* are genetically variable and distinct, we recommend that seed collection and sowing be conducted within rather than among populations. As well, seed collections should be made over multiple years to capture the genetic variation in the seed bank. On the basis of our work, we suggest that sowing and collection of seeds reflect historical hydrology, and that populations that may be hydrologically isolated, such as those within vernal pools, be maintained intact. Where human activities have impeded overland flows, site-wide sowing of seed collected from throughout the population may simulate historical patterns of seed movement.

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Appendix 1. ISSR primers used in study. An asterisk (*) indicate a *Chloropyron molle* subsp. *hispidum* specific band. A superscript caret (^) indicates a *Chloropyron palmatum* specific band.

Primer	Annealing temp °C	Informative bands (bp)								Sequence 5′–3′
807	54	330	370^	475	700	825	900			AGAGAGAGAGAGAGAGT
809	50	525*	550	730	830	870*				AGAGAGAGAGAGAGAGG
810	54	500	620*	900	950					GAGAGAGAGAGAGAGAT
811	54	400	790							GAGAGAGAGAGAGAGAC
818	54	580	720	770	900	1050	1130	2000*		CACACACACACACACAG
823	54	550	1000	1270*	2000					TCTCTCTCTCTCTCTCC
825	50	770	800	840	1900					ACACACACACACACACT
826	50	590	610*	670*	710	1130*	1300			ACACACACACACACACC
827	54	510	530*	600	770	1050	1400	1700	2000	ACACACACACACACACG
834	54	900	2000							AGAGAGAGAGAGAGAGYT
835	50	470	610							AGAGAGAGAGAGAGAGYC
836	54	870	1150*	1600	1750					AGAGAGAGAGAGAGAGYA
841	50	410^	1200	1800						GAGAGAGAGAGAGAGAYC
844	50	1170								CTCTCTCTCTCTCTCTRC
848	54	230	310	560	720	870^	925	1125*	1460	CACACACACACACACARG
849	50	1050	1160	1900*	2100*					GTGTGTGTGTGTGTGTYA
855	50	550	1200	1230*	1370					ACACACACACACACACYT
856	50	650^	775	830*	1200*					ACACACACACACACACYA
857	50	470	700*	920	1100	1200				ACACACACACACACACYG
860	50	600^	700*	900*	1270^	1500				TGTGTGTGTGTGTGTGRA
876	50	520	770	1250						GATAGATAGACAGACA
884	50	600	660	830	870					HBHAGAGAGAGAGAGAG
885	54	530	660	700	950					BHBGAGAGAGAGAGAGA
886	54	440*	525	757	1150	1200	1400			VDVCTCTCTCTCTCTCT
887	54	530	570	1000	1200					DVDTCTCTCTCTCTCTC
888	50	1070	1130*							BDBCACACACACACACA
889	50	750*	790^	810*	925*	1650*				DBDACACACACACACAC
899	50	575	850							CATGGTGTTGGTCATTGTTCCA

Appendix 2. RAPD primers screened in study.

Primer	Annealing temp. °C	Informative bands (base pairs)					Sequence 5′–3′
A04	42	570					AATCGGGCTG
A10	42	700	800	1600			GTGATCGCAG
A11	42	1500					CAATCGCCGT
B06	42	570	700	850	900	950	TGCTCTGCCC
B10	42	600	650				CTGCTGGGAC
F06	42	325	700				GGGAATTCGG
G03	42	560	700				GAGCCCTCCA
G18	42	850					GGCTCATGTG
H02	42	650	700				TCGGACGTGA
H03	42	750	900				AGACGTCCAC
H04	42	750	800				GGAAGTCGCC
H19	42	1300					CTCGACCAGCC
212	42	625					GCTGCGTGAC

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LATE SUMMER FOG USE IN THE DROUGHT DECIDUOUS SHRUB, *ARTEMISIA CALIFORNICA* (ASTERACEAE)

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ABSTRACT

Coastal fog affects many California plant species and can be critically important to species that experience periodic drought. Drought-deciduous species in particular rely on water availability to maintain their leaves during the summer. To determine fog water use in drought-deciduous plants, this study manipulated access to fog drip and measured the water relations of the common shrub, *Artemisia californica*, near Santa Barbara, CA. Measuring the stable isotope ratio of hydrogen and oxygen, this study found that *A. californica* uses fog water in the late summer months when fog is present. This additional water increased plant water content but had no effect on pre-dawn xylem pressure potential. While climatic variability inhibits reliable fog input to *A. californica* in Santa Barbara, this species can use fog water opportunistically and benefits from large fog events during the summer drought.

Key Words: Artemisia, drought, drought-deciduous, fog, stable isotopes, water relations.

In arid ecosystems, water is often the most limiting factor for plant survival and growth. This water generally comes in the form of rainfall; however, in coastal regions fog water can act as a strong influence on plants (Klemm et al. 2012). Fog provides a significant amount of water to plants in regions as distinct as the Atacama Desert of Chile (Cereceda et al. 1999) and Coastal Redwoods of California (Limm et al. 2009). Ecological studies of fog have explored the response of many plant types to fog water inputs (Corbin et al. 2005, Fischer et al. 2009, Limm et al. 2009, Berry and Smith 2012, Vasey et al. 2012, West et al. 2012). However, research has largely ignored drought-deciduous species, whose leaf phenology responds directly to seasonal water availability. Drought-deciduous plants drop their leaves during seasonal periods of drought as a means of conserving water (Harrison et al. 1971). In coastal California, fog tends to occur in the summer months during peak drought (Williams 2009). This additional water could provide significant physiological benefits for drought-deciduous shrubs along the California coast.

The most common drought-deciduous species along the California coast is *Artemisia californica* Less. (Harrison et al. 1971). This shrub species has high transpiration rates due to weak stomatal control and a thin cuticle (Harrison et al. 1971, Poole and Miller 1975). During periods of summer drought, *A. californica* will shed leaves as a means of reducing water loss. Previous research suggests that the rooting systems of *A. californica* are shallow compared to evergreen species that grow in the same environment (O'Leary 1990). This enables *A. californica* to respond rapidly to rainfall events but also reduces drought tolerance (Poole and Miller 1975). Considering the weak transpirational control and shallow rooting system of *A. californica*, the acquisition of late summer fog could provide significant physiological benefits if the plants are capable of taking up the fog water.

Fog can affect the water budget of *A. californica* through foliar uptake or through fog drip. Fog drip occurs when water vapor from a low-lying cloud condenses on plant material and then drips into the soil where it can be taken up by the roots. Foliar uptake, or the absorption of water into the plant directly through the leaves, can also provide some physiological benefits (Limm et al. 2009), but appears to be short-lived and has yet to be effectively quantified. As *A. californica* is drought-deciduous in the late summer, foliar uptake is unlikely to affect the shrub as there are few leaves for water to enter. However, the shallow rooting system of *A. californica* may allow this species to take advantage of fog drip that collects in the top layer of soil. In this study, we address the question: Can *Artemisia californica* access fog water and if so, does it affect plant water relations? We used the natural abundances of stable isotopes of water extracted from the xylem of the shrubs before and after fog events to evaluate whether

plants could take up fog. Simultaneously, we experimentally excluded fog drip from one set of shrubs using careful placement of tarps. We hypothesized that *A. californica* shrubs exposed to fog drip would experience an increase in their water content and water potential compared to plants from which fog drip was excluded.

Methods

Study Site

This study was conducted at Coal Oil Point Reserve (COPR), a part of the University of California Natural Reserve System, located approximately two miles west of the University of California Santa Barbara campus in Santa Barbara County, California (34 24′N, 119 52′W). Mean precipitation is 441±8 mm of rain per year with rainfall typically occurring between October and May. Mean temperatures fall between 6°C in January to 24°C in August (UCNRS 2014). This study took place from May to October in 2011 and August to September in 2012. Precipitation data were obtained from the COPR meteorological station (Roberts et al. 2010). Precipitation during the 2010–2011 rain year was higher than average (654 mm of rain), whereas 2012 was a drier year than average (282 mm of rain). Fog was quantified using fog collectors modified from a previous design (Fischer and Still 2007). This study took place in an area with interspersed patches of California sage scrub and grassland. The soil is Concepcion fine sandy loam with intrusions of clay.

Field Sampling

To quantify the effects of fog drip, fog water was excluded from the soil below shrub canopies using plastic tarps in the summers of 2011 and 2012. Fog drip exclusion was done in a manner similar to the precipitation exclusion experiments described in Breshears et al. (2008). In 2011, six adjacent *A. californica* shrubs were treated by placing tarps from the base of the stems to several feet beyond the edge of the canopies. The tarps were sealed together with waterproof adhesive tape to form a large rectangular matted area below the six treatment shrubs. The large tarps were removed prior to the first fall rain event in another six adjacent shrubs were left without tarp as control plants. We measured xylem pressure potential (XPP) and plant water content (WC) for each individual shrub. Xylem pressure potential measurements were taken before dawn, between 3:00 and 4:00 a.m. (pre-dawn) and between 1:00 and 3:00 p.m. the next day (midday) on each sampling date. Stem samples were bagged, placed in a cooler and within the hour, measured for XPP in the lab using a Scholander-type pressure chamber (Model 1000, PMS Instrument Comp., Corvallis, OR). Midday XPP stem samples were weighed prior to the XPP measurement and subsequently placed in a drying oven for 48 hours at 80°C. Plant water content was calculated as the water weight divided by the dry weight of the plant tissue. WC samples averaged 2.1 g dry weight (±0.58 g). Data was collected monthly from May through October, for a total of six sampling dates.

In 2012, to avoid the problem of pseudoreplication, we selected eight treatment and eight control shrubs that were isolated (>5 m apart) and interspersed with one another in the same area. Tarps were laid underneath treatment shrubs from the stem base to several feet beyond the canopy. Measurements of all plants were taken every two weeks from August through September, for a total of five sampling dates. As in 2011, measurements included XPP and WC. All samples were collected at midday, between 1:00 and 3:00 p.m. At the end of the 2012 field season, 5 cm deep soil samples were taken from below both treatment and control *A. californica* plants. Cores were collected 5 cm from the base of the plant to measure gravimetric soil moisture content in the lab.

Only adult shrub individuals were selected for the experiment. All shrubs were 0.75–1 m in height and had a large canopy to withstand destructive sampling over a summer season.

Stable Isotopes

To track fog water into xylem tissue, we measured the stable isotopic ratios of hydrogen and oxygen (Dawson et al. 2010). In 2011, we collected water samples from rain, fog and groundwater to characterize the water sources available to *A. californica*. Each rain event was captured in a small Nalgene container at a location five miles east of the field site. Fog water was collected from a harp-string collector design modified from Fischer et al. (2007) every few weeks during the summer months. Rain and fog water were collected with a 2–3cm layer of mineral oil in the container to prevent evaporation. Ground water samples were taken from nearby wells established by the Cheadle Center for Biological and Ecological Restoration. All water samples were run through a cellulose filter to remove particulate matter before analysis on a Los Gatos Research Liquid Water Isotope Analyzer (Model LWIA-24EP) at the California Institute of Technology.

Multiple fog (44) and rain (19) samples from 2011–2013 were used to construct a local meteoric water line (LMWL). The LMWL for Coal Oil Point Reserve is $\delta D = 7.456\delta^{18}O + 6.4349$, $R^2 = 0.94$. The line differs from the global meteoric water line (Gat 1996); however, this is

FIG. 1. Rain and fog accumulation for 2011 and 2012. The dark gray line represents rain and the light gray line represents fog water. The vertical dashed lines represent the dates of vegetation sampling for each year.

expected as the line includes water from fog and rain (Gonfiantini and Longinelli 1962).

Plant water samples consisted of suberized stem tissue from several of the *A. californica* shrubs. Once a month in July, August, and September of 2011, plant tissue samples were collected midday in sealed scintillation vials and placed on ice until they were brought back to the lab freezer (−25°C). Plant water samples were extracted using a cryogenic vacuum extraction line (Ehleringer et al. 2000) at UC Santa Barbara. These water samples were then shipped to the Stable Isotope Biogeochemistry Lab at UC Berkeley where they were analyzed on an Isotope Ratio Mass Spectrometer. Plant water samples were collected in 2012 but were not analyzed, as there was insufficient fog deposition during the summer of 2012.

We corrected all plant water samples for soil evaporation using the correction method developed by Corbin et al. (2005) in Northern California. Use of an evaporation correction is necessary for studies in semi-arid ecosystems, as the water used by plants has experienced evaporative fractionation prior to uptake. Plant samples were corrected back to the local meteoric water line for COPR. We then used a mixing model analysis with two isotopes and three sources (rain, groundwater and fog) for all plant water samples to determine the proportion of fog water used by plants (Phillips and Gregg 2001).

Analysis

Data were analyzed using JMP® Pro 11 (SAS Institute). We conducted a repeated measures analysis for plant water content and predawn XPP over time to compare the effects of the matting treatment within each year. For WC we used a residual error covariance structure as it had the lowest value for the AICc criteria, for five of the six sampling dates (excluding October). For XPP we used an AR(1) covariance structure as it had the lowest value for the AICc criteria. We used a one-way ANOVA to analyze the difference in soil moisture between treatment and control. Differences in fog proportion by date were compared with a pairwise Student's t-test.

RESULTS

Fog and Rain Inputs

Quantities of rainfall and fog water collected were both greater during 2011 than 2012 (Fig. 1). In 2011, a total of 1693 ml of fog water was collected from 5/6/2011 through 10/25/2011, whereas only 188 ml was collected from 7/1/2012 through 9/27/2012. In 2012, fog data collection began two months later than in 2011; however, there was much less late summer fog in 2012. In 2011, total fog collected was more than nine times greater than that of 2012. The only rain event to occur during the treatment period was a 30 mm rain event on 6/6/2011. There was rain on 10/5/2011; however, the tarps had been removed just prior to this event.

The isotopic signature of fog water at Coal Oil Point Reserve was more enriched in the heavy isotopes of Hydrogen and Oxygen compared to both rain and groundwater (Fig. 2) as is typical of fog water in other ecosystems (Scholl et al. 2010). Rain and groundwater were not significantly different from one another.

Fog Water Isotope Analysis

The isotopic signature of *A. californica* stem water varied across the summer of 2011; it was initially depleted of heavy isotopes in the mid-summer and became enriched in September. Both treatment and control plants experienced an increase in the proportion of fog water present

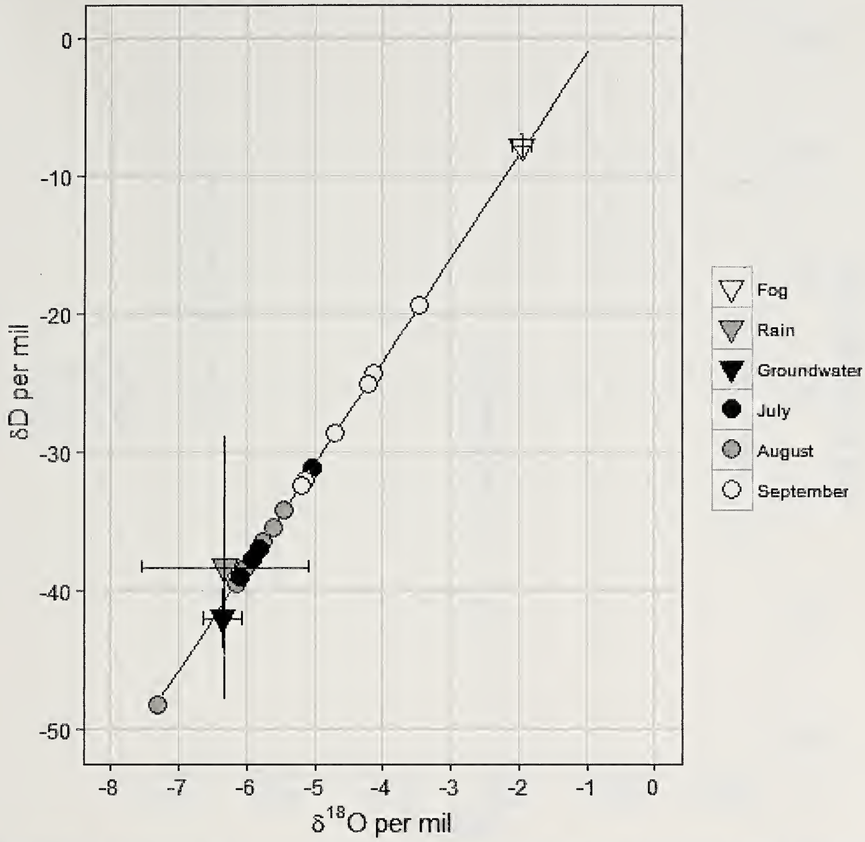

FIG. 2. The isotopic signatures of water and *A. californica* stem tissue at Coal Oil Point Reserve. Fog is isotopically enriched in the hydrogen and oxygen isotopes (white triangle). Rain and groundwater are depleted (gray and black triangle, respectively). Plant water samples were corrected to the local meteoric water line (black line). Error bars are the standard error associated with source water isotopic values.

in their stem tissue in September. There is a significant difference between September and both July and August (July: $P = 0.0093^*$, August: $P = 0.0008^*$) when treatment and control plants are combined (Fig. 3).

Plant Water Status

In 2011 the plant water content (WC) of both control and fog drip exclusion plants decreased during the summer, and increased after the first fall rain (Fig. 4). A small rain event on June 6th temporarily increased WC of both control and fog drip exclusion plants. A repeated measures analysis of WC for the five sampling dates between June and October found that there was a significant effect of time ($P < 0.0001^*$) with WC generally decreasing throughout the dry season. The treatment effect alone was not significant ($P = 0.4258$), but there was an interaction effect of treatment*time ($P = 0.0004^*$). In 2012 the difference in WC between treatment and control was non-significant ($P = 0.2786$) and there was no interaction effect with time ($P = 0.8677$).

The 2011 pre-dawn xylem pressure potential (XPP) of both groups decreased during the summer and increased after the first fall rain event (Fig. 5). A repeated measures analysis of XPP yielded a significant effect of time ($P < 0.0001^*$) but no significant effect of treatment ($P = 0.597$). There was no significant interaction effect of the treatment over time ($P = 0.193$). For midday XPP, there was a significant effect of treatment ($P = 0.028^*$) as the control plants had slightly higher water potential at each sampling date. This slight difference was observed from the beginning of the experiment as the difference between treatment and control values did not change over time ($P = 0.975$). This indicates that the difference observed was an artifact of the individual plants selected for the experiment, not an effect of the treatment. In 2012 there was no effect of treatment ($P = 0.902$) or treatment over time ($P = 0.340$).

The soil moisture beneath the fog drip exclusion and control plants was significantly different at the end of the 2012 treatment ($P = 0.011^*$), with the fog drip exclusion plants having an

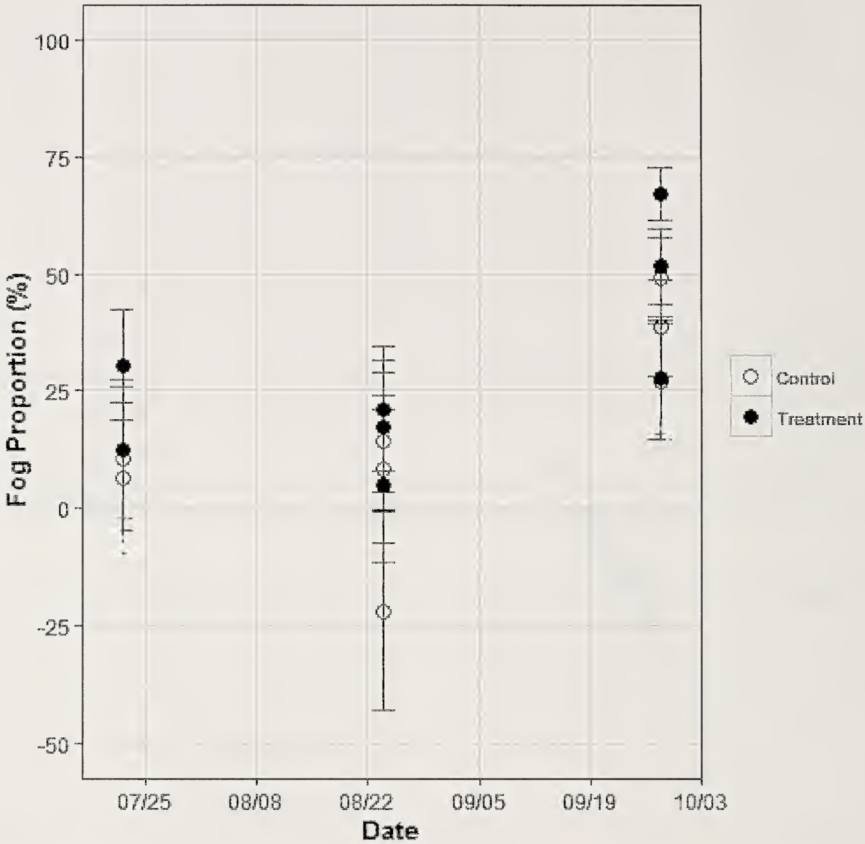

FIG. 3. Phillips and Gregg's (2001) mixing model results for fog proportion in stem water for 2011. Both treatment and controls plants shifted towards fog in September. Each point with bars is an individual plant with the mean and standard error of fog proportion according to the model.

average soil moisture of 4.66% (±0.66%) and the control plants an average 4.08% (±0.56%).

Discussion

The results presented here support the hypothesis that *Artemisia californica* uses fog water in the late summer. This additional water appears to increase plant water content for individual *A. californica* shrubs.

A significant fog event (128 ml over four days) before the September sampling date likely caused the observed difference in WC in September of 2011 (Fig. 4). No rain occurred from August to September, further supporting the idea that the increase in WC of control plants was due to the large fog event that occurred in early September (Fig. 1). While control and treatment plants differed in their WC, the water isotopes in their stem tissue both reflected a higher proportion of fog water in September of 2011 (Fig. 3). This suggests that the treatment plants, despite the attempted exclusion of fog drip, were incorporating fog water into their stem tissue between August and September of 2011. This presence of fog water in treatment plants, if not through root uptake, may be due to foliar uptake. Foliar uptake of fog has been found in numerous plant species, including California shrub species (Limm et al. 2009). If this is the case, foliar uptake of fog was not enough to alter WC in the treatment plants, but was detected in the water isotopes of all shrubs. For control plants, root access to fog water may have increased WC in September, but it had little effect on the pre-dawn XPP (Fig. 5). These results suggest that although *A. californica* could acquire fog through multiple mechanisms, root uptake of fog drip can improve the water budget of this drought-deciduous shrub during periods of significant fog deposition.

The similarity in pre-dawn XPP between control and treatment plants may be explained by a difference in soil water content below the tarps. The soil moisture data from 2012 suggests that the tarps had the unintentional effect of reducing soil evaporation, as the control plants had significantly lower soil moisture than the treatment plants. In 2011, this would explain the

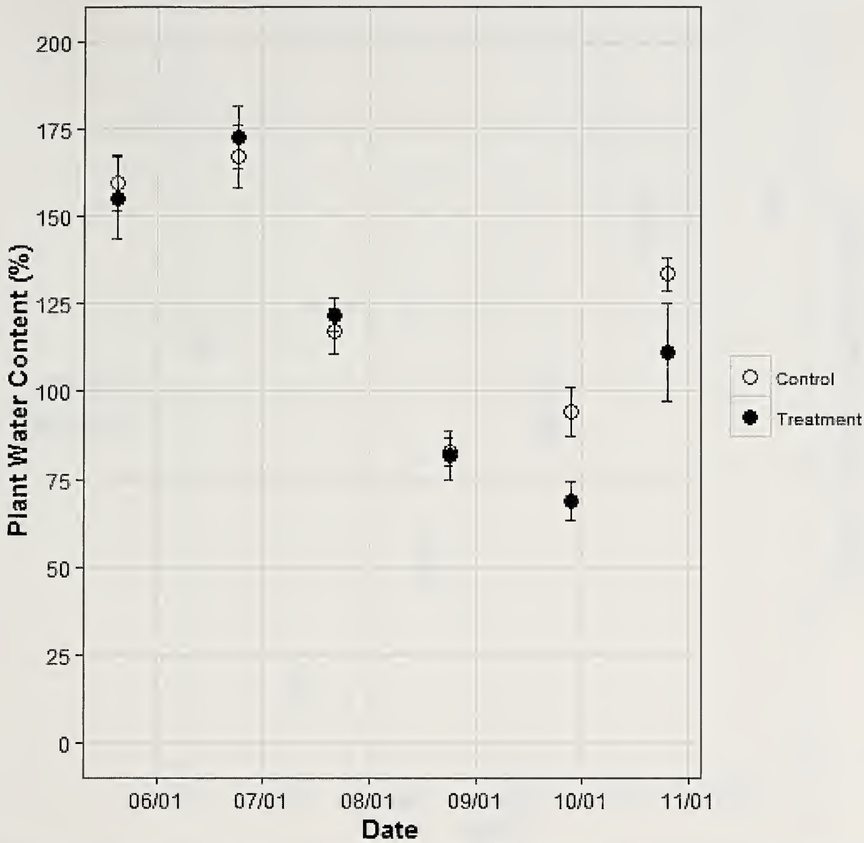

FIG. 4. Plant water content (%) of *A. californica* during the 2011 summer sampling period. Error bars represent plus/minus one standard error.

lack of difference between the XPP of the treatment and control individuals (Fig. 5). If reduction in soil water evaporation increased the amount of water available to treatment plants, it could result in no observable difference in pre-dawn XPP. Alternatively, by the late summer both treatment and control plants may no longer have the ability to effectively conduct water. The late summer XPP observed in this study is similar to the values observed in Jacobson et al. (2007) where there was 75% loss of hydraulic conductivity in *A. californica* during the dry season. It is possible that although *A. californica* can take up fog water, hydraulic conductivity is too low to alter pre-dawn water potential inside stems.

Overall, this study provides the first evidence of fog water use by a drought-deciduous shrub, and attempts to understand the importance of fog drip during the seasonal drought period in coastal southern California. Dropping leaves in the summer is costly for plants and is likely triggered by water availability (Harrison et al. 1971). Fog inputs could prolong leaf lifespan and enable greater carbon assimilation for species such as *A. californica*. Our results suggest that fog increases *A. californica* water content through roots and possibly foliar uptake. However, the effects of fog appear to be temporary and do not provide a consistent summer water resource for coastal California's drought-deciduous shrub species.

The interannual variability of fog deposition observed in this study (Fig. 1) is consistent with long-term cloud records (Williams 2009). In coastal California regions with consistent and large quantities of fog deposition, fog can contribute greatly to plant water relations (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012). Plant species in the Santa Barbara region are unlikely to depend on summer fog as a water source, though some may opportunistically use fog water during the summer drought. With predictions of a warmer climate in California (Cayan et al. 2008), the results from this study may provide a window into future climate-plant interactions for more northern shrub-dominated ecosystems along the California coast.

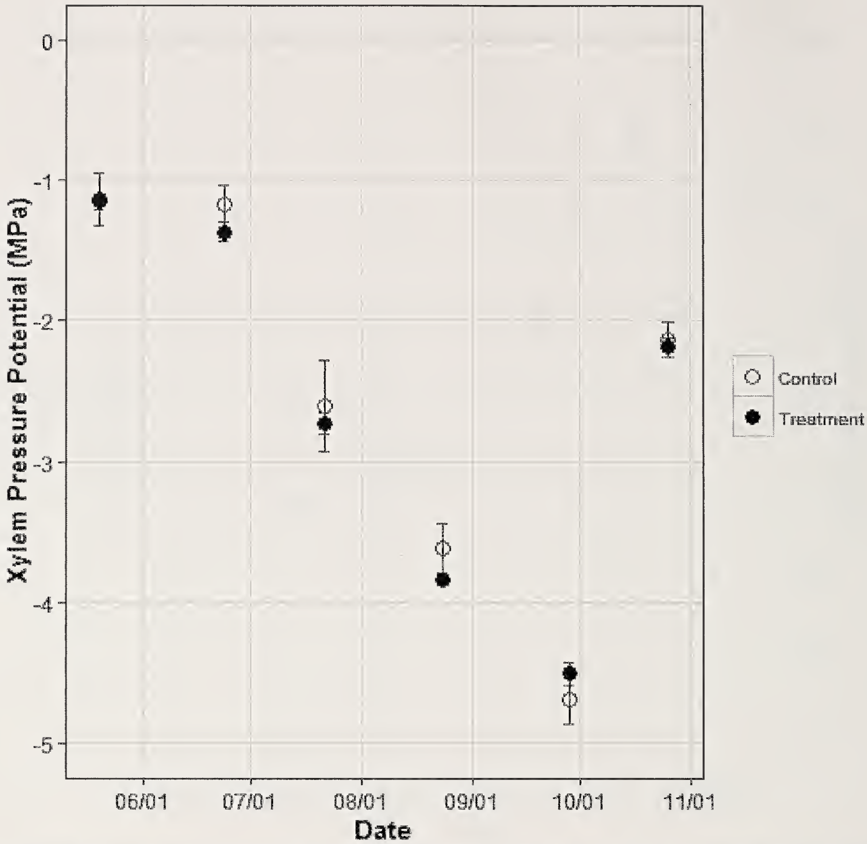

FIG. 5. Pre-dawn xylem pressure potential of *A. californica* during the 2011 summer sampling period. Values represent means of the six plants per treatment. Error bars represent plus/minus one standard error.

ACKNOWLEDGMENTS

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ERYTHRONIUM SHASTENSE (LILIACEAE), A NEW SPECIES FROM NORTHERN CALIFORNIA

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Abstract

Erythronium shastense D. A. York, J.K. Nelson, & D. W. Taylor is described as a new species restricted largely to limestone outcrops near Shasta Lake, Shasta County, California. Style, leaf, and anther characters are used to distinguish *E. shastense* from the similar *E. californicum* and *E. helenae.*

Key Words: *Erythronium* section *Pardalinae,* fawn lily, foothill woodland, limestone, McCloud River Arm, northern California, Pit River Arm, rare endemic plant species, Shasta Lake.

The genus *Erythronium* consists of ~29 species, with 17 taxa known from western North America (Allen and Robertson 2002, Clennett 2014). The 15 California taxa (Allen 2012) form two groups; the plants with strongly mottled leaves (*Erythronium* section *Pardalinae* of Applegate 1935) generally occurring at lower elevations, and plants without to very faint mottling occurring at higher elevations (*Erythronium* section *Concolorae* Applegate) (Shevock and Allen 1997). An unidentified *Erythronium* of sect. *Pardalinae* was encountered by the third author in 1993 on limestone outcrops adjacent to the McCloud River Arm of Shasta Lake (<30 meters above spillway elevation) at 350 meters elevation. The second author noticed and photographed the same unknown *Erythronium* on the road to Hirz Mountain in 2010. In 2012, the first author independently encountered this novel *Erythronium* in the same watershed, and noted its distinction from congeners. Subsequently, recent collections and photographs of this unique *Erythronium* from limestone outcrops circumscribing Shasta Lake, confirm occurrences at Hirz Mountain, North Gray Rocks above Shasta Caverns, and at Brock Creek adjacent to the Pit River Arm of Shasta Lake (Fig. 1). The discovery of these populations led to our recognition of this new taxon.

Taxonomic Treatment

Erythronium shastense D. A. York, J. K. Nelson, & D. W. Taylor sp. nov. (Figs. 2–4). —Type: USA, California, Shasta Co., Shasta-Trinity National Forest, North Gray Rocks adjacent to the McCloud River Arm of Shasta Lake, N-facing slopes on a limestone outcrop above Shasta Caverns, with *Achillea millefolium* L., *Adiantum* L. sp. nov. (ined.), *Boechera breweri* (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz, *Ceanothus cuneatus* (Hook.) Nutt., *Cercis occidentalis* Torr. ex A. Gray, *Cercocarpus betuloides* Nutt., *Cheilanthes cooperae* D.C. Eaton, *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray, *Cystopteris fragilis* (L.) Bernh., *Erythranthe taylori* Nesom, *Holodiscus discolor* (Pursh) Maxim, *Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E. Wollenw., *Pinus sabiniana* Douglas ex G. Don, *Sedum spathulifolium* Hook., *Selaginella wallacei* Hieron, *Toxicodendron diversilobum* (Torr. & A. Gray) Green, and *Umbellularia californica* (Hook. & Arn.) Nutt., 40.80035°, -122.27475°, 865 m (2840 ft), 10 April 2013, *Dana York 3155* (holotype: CAS; isotypes: JEPS, US).

Distinct from *E. helenae* Applegate in its longer style, leaves that are as much as 6 cm longer, and stamens as much as 3 mm longer. Distinct from *E. californicum* Purdy in its bright yellow anthers, larger leaves, and declined style.

Bulb 2.5–9.5 cm long, slender, ovate to elongate, propagating by sessile offsets protruding from the bulb coat. **Leaves** 2, white or brown mottled, 12–26 cm long, 1.7–6.5(11) cm wide, lanceolate to elliptic or ovate, margins undulate. **Scapes** (13)24–30 cm tall; **flowers** 1–3, spreading (nodding). **Tepals** 6, slightly recurved to spreading or campanulate, lanceolate, often pink in bud, tips acute to acuminate, 24–41(45) mm long, 6–15 mm wide, white, fading pinkish to purplish after anthesis, with a 7–9 mm long golden yellow

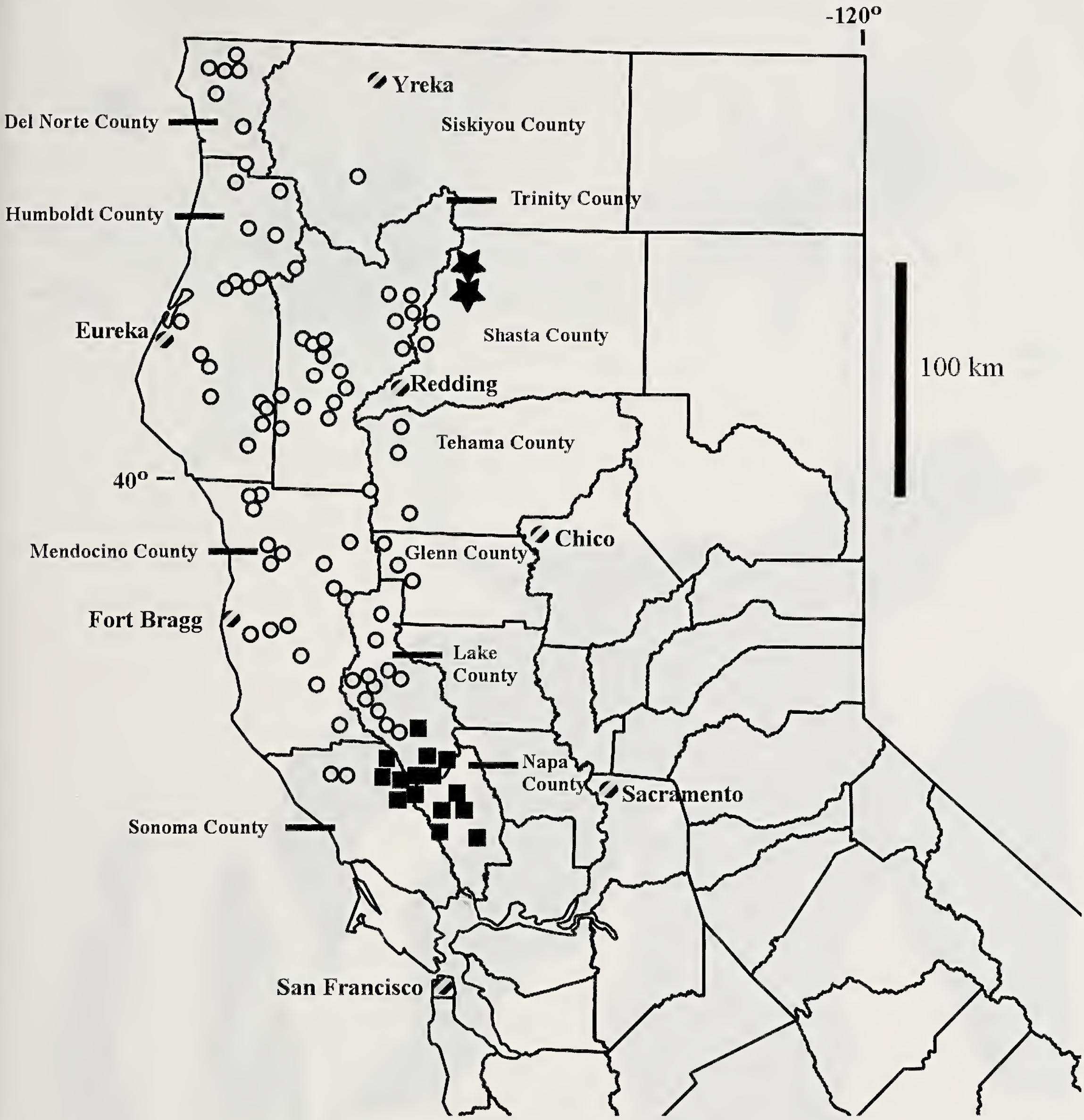

FIG. 1. Map of northern California (with county boundaries) showing the distribution of Consortium of California Herbaria *Erythronium* specimens. ★ = *Erythronium shastense*, ○ = *Erythronium californicum*, ■ = *Erythronium helenae*.

zone at base. Inner three tepals with saclike appendages at base on adaxial surfaces. **Stamens** unequal in two series, 9–12(16) mm long. **Filaments** 5–7(11) mm long, 0.2–0.5 mm wide, white to yellowish; **anthers** 4–5 mm long, yellow. **Style** clavate, 8–14 mm long, white, declined; **stigma** entire to short lobed, the lobes <2 mm. **Capsules** obovoid, 1.3–3.2 cm long.

Paratypes: USA, CALIFORNIA. **Shasta Co.:** Hirz Mountain road, off Gilman Road, east of I-5, north of Shasta Lake, growing on limestone outcrop, roadside, fill slope in shade, on a north aspect, UTM NAD 83 Zone 10 562457E, 4527762N, 3344 ft, 15 April 2014, *Nelson & Lenz 2014-010* (CHSC, RSA); Shasta-Trinity National Forest, along Gilman Road (Road 7H 009) about 0.4 road miles west of the entrance road to Dekkas Rock Campground, TRS 35N3W19, NAD 83 40.87528°, -122.24089°, 1219 feet (371 m), 9 April 2014, *Taylor 21465* (HSC, CHSC, RSA); Gilman Road, east of I-5, north of Shasta Lake above Jennings Creek, UTM NAD 83 Zone 10 564277E, 4528596N, 1200 ft, 14 March 2014, *Nelson et al. 2014-005* (CHSC, HSC, RSA); Shasta-Trinity National Forest, Peak 2968 just north of North Gray Rocks adjacent to the

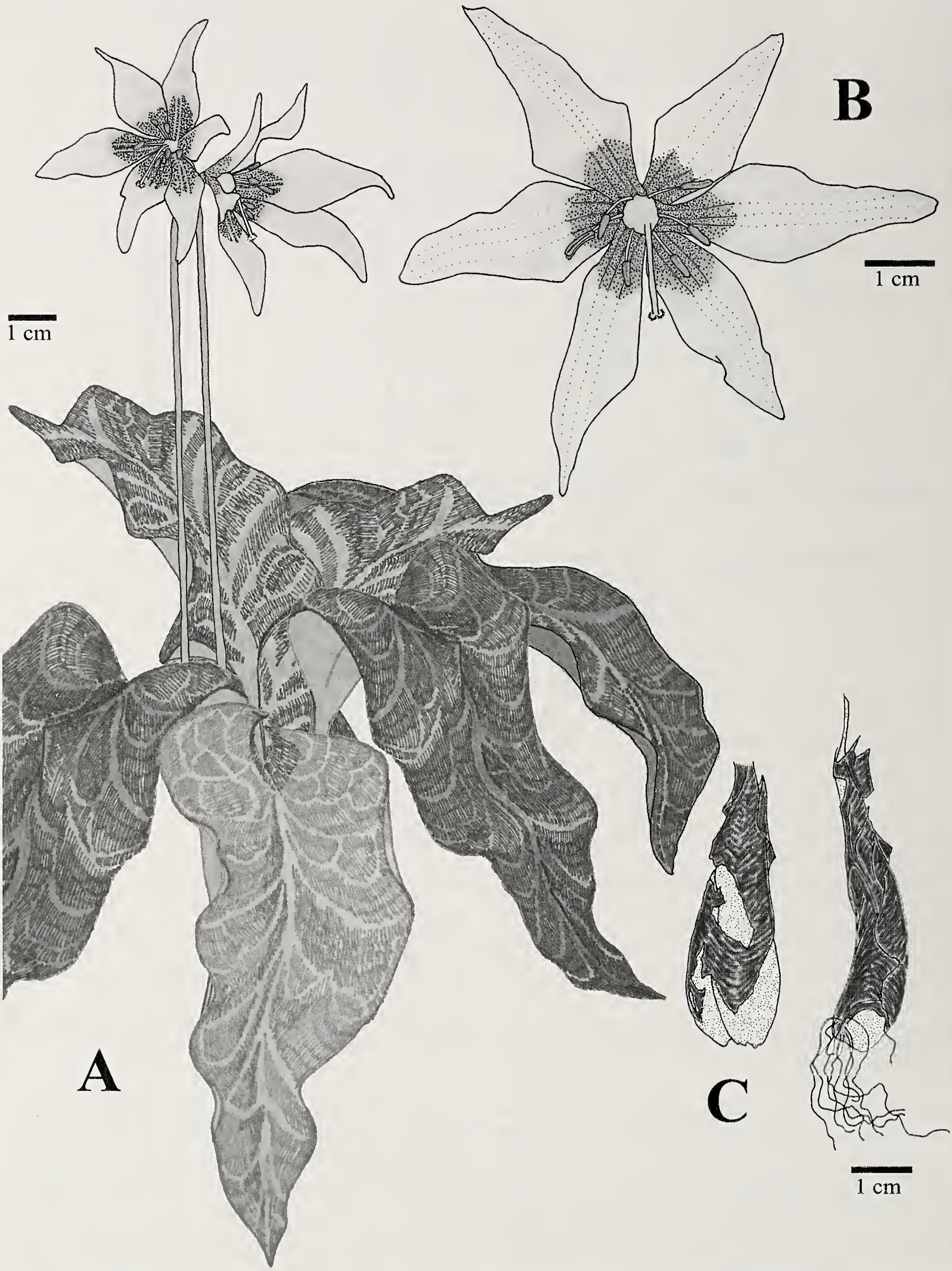

FIG. 2. *Erythronium shastense*. A. Habit, with plant having two flowers above mottled leaves. B. Flower, with declined style. C. Bulbs. Illustrations by Diana D. Jolles.

FIG. 3. *Erythronium shastense*. A. Two adjacent plants in limestone habitat. B. Flowers showing declined styles. C. Bulbs from several plants. D. Pendent buds.

McCloud River Arm of Shasta Lake, shaded limestone rock shelves and crevices, 40.80422°, -122.27111°, 900 m (2960 ft), 19 May 2012, *York 3112* (HSC); 1 mile south of McCloud River bridge along road between Ellery Creek and Pine Point Campground, 350 m, 5 March 2003, *Taylor & Reyes 18467* (JEPS100448, UC1755122); McCloud Arm Lake Shasta, along road between Ellery Creek and Pine Point Campground (ca. 1 mile south of McCloud River bridge), 350 m, 17 March 1993, *Taylor 13302* (JEPS96527); 15 miles northwest [sic, northeast] of Redding, 21 April 1935, *Rose 30* (JEPS61880).

ETYMOLOGY

The specific epithet is named for Shasta Lake, Shasta County, where the only known populations occur in close proximity to the reservoir. The suggested common name is Shasta fawn lily.

FIG. 4. *Erythronium shastense* watercolor. Illustration by Paul C. Reinwand © 2015.

DISTINGUISHING CHARACTERISTICS

Erythronium shastense has large (to 26 cm long) mottled leaves and large spreading flowers (tepals to 41 mm long). At anthesis, the style tends to be strongly declined and away from the anthers, resulting in herkogamy. The anthers are bright yellow when they first dehisce. Plants grow in clumps where enough soil exists in cracks and ledges on the carbonate rock substrate. The plant's leaves and flowers easily stand out against the gray limestone rock. Flowers appear in late winter or early spring when occurrence of rainfall is still very likely. During the summer *E. shastense* foliage dies back to its bulb until the following winter and the start of another year's cycle.

TAXONOMIC RELATIONSHIPS

Of the three strongly supported lineages within *Erythronium* (Clennett et al. 2012), all California taxa fall within an unranked "western North American clade", which has moderately good bootstrap support on combined molecular and morphological phylogenetic analysis (Allen et al. 2003, Clennett 2014). Clennett et al. (2012) found weak support for lineages within the western North American clade. *Erythronium shastense* is morphologically most similar to *E. helenae* Applegate and *E. californicum* Purdy (Table 1). However, *E. helenae* and *E. californicum* often pair together in a clade with *E. hendersonii* S. Watson, *E. howellii* S. Watson, *E. citrinum* S. Watson, and *E. multiscapideum* (Kellogg) A. Nelson & P. B. Kennedy in phylogenetic studies by both Clennett et al. (2012) and Allen et al. (2003), and are keyed in similar fashion (Allen and Robertson 2002). Clennett (2014) recognizes *E. californicum* as having two races; one form with smaller leaves, flowers, and fruits which he attributes to populations from the Trinity Mountains (and which also occur in the High North Coast Ranges) and a larger form occurring in outer North Coast regions of northwest California. Recognition of *E. shastense* now requires that the phylogeny of the North American clade be revisited.

One subtle but significant feature of *E. shastense* is the orientation of flowers at anthesis. Many taxa of *Erythronium* L. offer flowers that are pendant atop a strongly geniculate (distally recurved) scape, with the dehiscing anthers and receptive style dangling below. By contrast, at full anthesis, *E. shastense* flowers are mostly oriented laterally (spreading), with the tepals forming a parabola that is significantly more often oriented horizontally (Figs. 2–4). In bud, the unopened flowers of *E. shastense* are pendant as in congeners; flower orientation features are largely absent on herbarium specimens. The spreading to nodding flowers of *E. shastense* differ somewhat from congeners, including pendant-flowered *E. californicum*, its nearest geographic neighbor—most species of *Erythronium* have nodding or pendant flowers at anthesis, an orientation that provides protection from precipitation potentially damaging flower parts or eroding pollen from the open anthers. Style position is possibly related to flower orientation. Unlike *E. californicum* where the style is exserted well beyond the anthers, *E. shastense* and *E. helenae* achieve herkogamy with declined (having a positive gravitropic response) styles presenting the stigma below and away from the anthers.

In practice, classifications of *Erythronium* (Applegate 1935, Matthew 1992, Allen and Robertson 2002, Allen 2012, Clennett 2014) have treated constituent entities as full species, rather than recognizing closely related, morphologically overlapping, or demonstrated sister taxa as sub-

TABLE 1. COMPARISON OF DIAGNOSTIC CHARACTERS AMONG *ERYTHRONIUM* SPECIES OF CALIFORNIA.

	Leaf blades			Inflorescences	Tepals		Filaments		Anthers	Style	Stigma
Erythronium taxon	Distinctly mottled white or brown	Length (cm)	Width (cm)	# of flowers per scape	Color	Color at base	Color	Width (mm)	Color	Length (mm)	Lobes (mm)
E. shastense	Yes	12–26	1.7–6.5(11)	1–3	White	Yellow	White to ± yellow	<0.6	Yellow	8–14 (declined)	0–2
E. californicum	Yes	7–15	2.5–5	1–3	White to cream	Yellow	White	<0.8	White to cream	10–15	0–2
E. citrinum var. *citrinum*	Yes	9–15	1.5–4	1–3	White	Yellow	White to pinkish	<0.8	White to cream	6–10	0–1
E. citrinum var. *roderickii*	Yes	9–15	1.5–5	1–3	White	Yellow	White to pinkish	<0.8	Pink to dark red	6–10	0–1
E. grandiflorum subsp. *grandiflorum*	No	5–20	1.4–5	1(3)	Yellow	Pale yellow	White	<0.8	Cream to yellow (dark red)	10–15	2–4
E. helenae	Yes	10–20	0.7–2.2	1–3	White	Yellow	± Yellow	<0.8	Yellow	5–8 (declined)	0–1
E. hendersonii	Yes	10–25	2–4.5	1–4	Violet to pink	Dark purple	Purple	<0.8	Pale brown to purple	6–8	0–1
E. klamathense	No	6–17	1.5–2.5	1–3	White	Yellow	± Yellow	<0.8	White	4–9	0
E. multiscapideum	Yes	4–15	1–2.5	1–4	White	Yellow	White	<0.8	White to cream	10–13	1–4
E. oregonum	Yes	10–22	3–6	1–3	White to cream	Yellow	White	2–3	Cream to yellow	10–13	3–6
E. pluriflorum	No	7–30	1.5–6	1–10	Yellow	Yellow	Yellow	<0.8	Yellow	6–8	0–1
E. purpurascens	No	6–15	1–2.5	1–6	White	Yellow	Yellow	<0.4	Cream to yellow	4–5	0
E. pusaterii	No	10–35	2–6	1–8	White	Yellow	White	<0.8	Yellow	7–10	0–1
E. revolutum	Yes	10–25	3–6	1–3	Violet-pink	Yellow bands	White to pink	2–3	Yellow	12–18	4–6
E. taylorii	No	18–35	4–9	1–8	White	Yellow	Yellow	<0.4	Cream	9–11	0–1
E. tuolumnense	No	15–35	4–8	1–5	Yellow	Yellow	White to cream	0.4–0.6	Yellow	8–10	0–1

species. We thus treat *E. shastense* by this same method as a full species.

Phenology

Erythronium shastense flowers from February to April, developing mature fruits in May. Leaves quickly wither with the onset of hot, dry weather in May.

Distribution, Habitat, Ecology, and Conservation Implications

Erythronium shastense grows in shallow soils on shelves and in crevices in the calcareous rock outcrops circumscribing the McCloud River and Pit River arms of Shasta Lake (Fig. 5). It is restricted largely to the McCloud and Hosselkus limestone formations formed between the Early Permian and Upper Triassic (Demirman and Harbaugh 1965). In the Shasta Lake region, the McCloud limestone formation outcrops form a narrow band approximately one km wide, extending for about 30 km in a north-south orientation (Demirman and Harbaugh 1965). *Erythronium shastense* plants are scattered about the north-facing or shaded limestone rock outcrops in forest and mixed woodland plant communities dominated by combinations of the following species: *Ceanothus cuneatus* Nutt. var. *cuneatus, Cercocarpus betuloides* Nutt., *Chrysolepis sempervirens* (Kellogg) Hjelmq., *Garrya fremontii* Torr., *Holodiscus discolor* (Pursh) Maxim., *Pinus sabiniana* D. Don, *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus chrysolepis* Liebm., *Q. garryana* Hook. var. *breweri* (Engelm.) Jeps., *Q. kelloggii* Newb., *Toxicodendron diversilobum* (Torr. & A. Gray) Greene, and *Umbellularia californica* (Hook. & Arn.) Nutt. Known populations of *E. shastense* have one or more of the following associates: *Adiantum* sp. nov. (in press), *Ageratina shastensis* (D. W. Taylor & Stebbins) R.M. King & H. Rob., *Boechera breweri* (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz, *Cercis occidentalis* A. Gray, *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray var. *californicus* (J. M. Coult. & Rose) Jeps., *Delphinium nudicaule* Torr. & A. Gray, *Erythranthe taylori* Nesom, *Myriopteris cooperae* (D. C. Eaton) Grusz & Windham, *Sedum spathulifolium* Hook., and *Selaginella wallacei* Hieron.

Like *E. helenae* (Applegate 1933), *E. shastense* can form clumps due to bulb offsets (bead-like tissues arising from the bulb). This adaptation is well suited for taxa that tend to grow in rocky conditions with little soil development. Zonal soil development in such rocky habitats is limited; vascular plant establishment is restricted to cracks, fissures or solution pockets in limestone where organic matter accumulates, and where seeds find suitable conditions. The clumped growth habit of *E. shastense* is a functional trait adaptive to cliffs and such crevices.

Fig. 5. Limestone outcrop habitat for *Erythronium shastense*, with Shasta Lake in the background.

The distribution and abundance of *E. shastense* is doubtless incompletely known, but a substantial portion of suitable habitat has been floristically investigated in recent decades. The 1978 description of *Ageratina shastensis* (Taylor and Stebbins 1978) led the third author to continue to visit limestone outcrops in the Shasta Lake region, resulting in the 1992 discovery of *Neviusia cliftonii* Shevock, Ertter, D. W. Taylor (Shevock et al. 1992). Subsequent surveys, initiated by the second author to elucidate the habitat and rarity of *N. cliftonii* (Lindstrand and Nelson 2006), visited a large fraction of the regional limestone substrate sites without locating any additional *E. shastense* occurrences. It is possible that the surveys were timed too late in the growing season to detect *E. shastense* plants. Other recent spring surveys, targeting the recently described *Erythranthe taylori* (Nesom 2013), only detected two additional Shasta fawn lily occurrences. Adding *E. shastense* to the suite of limestone endemics of the Shasta Lake region strongly suggests that, going forward, comprehensive and fully-vouchered floristic exploration of the region is in order. Many limestone outcrops in this region are remote from roads, are on very steep slopes generally infested with poison oak, and are difficult to access. Consequently, floristic exploration of this region is incomplete.

Safford et al. (2005) rated *E. helenae* as a strong indicator of serpentine affinity, whereas *E. shastense* is a strong calciphile, these substrate preferences indicating divergence between the two species. Other *Erythronium* taxa that have an obvious affinity to a specific and regionally unique geologic substrate include *E. citrinum* S. Watson var. *citrinum* (serpentinite), *E. citrinum* var. *roderickii* Shevock & G. A. Allen (serpentinite), and *E. taylorii* Shevock & G. A. Allen

(metamorphic marine sediments) (Shevock and Allen 1997). *Erythronium shastense* and *E. helenae* are strongly allopatric, situated at, respectively, the north and south ends of the range of *E. californicum* (Fig. 1). *Erythronium californicum* has not been reported from Oregon: vouchers are known within 8 km of the state line (*Smith et al. 10274*, HSC74878) and might be expected to occur therein.

Because *E. shastense* is restricted to a few known occurrences, mostly on low-elevation limestone in northern California, around or near Shasta Lake, it is of conservation concern. It grows in sympatry with or near the following local endemic plants: *Adiantum* sp. nov. (ined.), *Ageratina shastensis, Erythranthe taylori*, *Neviusia cliftonii,* and *Vaccinium* sp. nov. (ined.). Past and current mining of limestone within potential habitat for *E. shastense* is a proximal threat factor. Other threats include planned reservoir expansion of Shasta Lake, road and trail maintenance/construction, invasive species (some known sites have dense *Rubus armeniacus* Focke), and any habitat changes due to climate change.

In 1935, the novel species of *Erythronium* described herein was first collected and filed as *E. californicum* Purdy by Mrs. C. F. Rose (*Rose 30*, JEPS6180). The Rose collection is labeled as "15 miles northwest of Redding" which places it in the area of Shirttail Peak, an area without limestone. We surmise that the collection actually came from 15 miles northeast of Redding, placing it in an area where limestone is a common substrate. The 1935 Rose collection was not accessioned at Jepson Herbarium until decades later and bears a typewritten label rather than an autographic one, suggesting that "northeast" might well have been recorded incorrectly as "northwest". *Erythronium californicum* was documented by the third author from Shirttail Peak in 2004 (*Taylor, Molter, and Engstrom 19102*, JEPS118209).

Key To California *Erythronium* With White or Brown Mottled Leaves

A revised key, after Allen (2012), based on California taxa with mottled leaves is provided below:

1. Filaments 2–3 mm wide; stigma lobed
  2. Tepals white with yellow base . . . . *Erythronium oregonum*
  2′. Tepals violet-pink with yellow base . . . . *Erythronium revolutum*
1′. Filaments <0.8 mm wide; stigma entire to lobed
  3. Tepals violet to pink with dark purple base . . . . *Erythronium hendersonii*
  3′. Tepals mostly white with yellow base
    4. Longest styles >10 mm
      5. Anthers yellow; style generally declined; largest leaves >20 cm long . . . . *Erythronium shastense*
      5′. Anthers white to cream; style straight; largest leaves ≤15 cm long
        6. Peduncle, when inflorescence has >1 flower, branched above leaves. . . . . *Erythronium californicum*
        6″. Peduncle, when inflorescence has >1 flower, branched near ground. . . . . *Erythronium multiscapideum*
    4′. Longest styles ≤10 mm
      7. Anthers yellow; style generally declined . . . . *Erythronium helenae*
      7′. Anthers white, cream, pink, brown, purple, or red; style straight
        8. Anthers white to cream . . . . *Erythronium citrinum* var. *citrinum*
        8′. Anthers pink to brown- or purple-red . . . . *Erythronium citrinum* var. *roderickii*

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A NEW SPECIES OF *VACCINIUM* (ERICACEAE) FROM THE SOUTHEASTERN KLAMATH MOUNTAINS AND THE SIERRA NEVADA, CALIFORNIA, WITH TWO SUBSPECIES

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ABSTRACT

Vaccinium shastense J. K. Nelson & L. Lindstrand III (Ericaceae) is described as a new species from interior California. This new species is most similar to *V. parvifolium* Smith but differs by its ciliate, inrolled leaf margins, much wider hypanthium scar, dark blue, glaucous, quickly deciduous fruits, greater seed count, and pitted seed surface sculpturing. Moreover, *V. shastense* and *V. parvifolium* are allopatric, occur in distinct habitats, and have distinct genetic characters. Two subspecies of *Vaccinium shastense* are described: **Vaccinium shastense** subsp. **shastense**, endemic to the southeastern Klamath Mountains in Shasta County, California, and **Vaccinium shastense** subsp. **nevadense** J. K. Nelson & L. Lindstrand III from the western slope of the Sierra Nevada, California. The new subspecies differ from one another in flower color, length of persistent calyx ring, growth habit, geographic range and habitat, and distinct genetic characters. *Vaccinium shastense* subsp. *shastense* and *Vaccinium shastense* subsp. *nevadense* are compared to morphologically similar taxa in California by inclusion of an updated species key.

Key Words: California endemic, Ericaceae, Shasta huckleberry, Sierra huckleberry, Sierra Nevada, southeastern Klamath Mountains, Vaccinium shastense subsp. shastense, Vaccinium shastense subsp. nevadense, western Shasta County.

An unusual *Vaccinium* was found in 1991 by the first author at Golinsky Mine, on the west side of Shasta Lake in western Shasta County, California, growing on acid mine drainage seeping from bedrock crevices. This *Vaccinium* most closely fit the description of *V. parvifolium* Smith with the exception of its obviously different, dark blue, glaucous fruits, and an anomalous habitat with high summer temperatures and very low humidity. Similar plants were found in 2003 and 2004 at several other locations in the southeastern Klamath Mountains around Shasta Lake, Shasta County, California. The unusual fruit color, combined with the facts that these Shasta County populations are disjunct from the nearest putative *V. parvifolium* populations by at least 64 km and that they occur in a much more xeric region and habitat, led us to suspect them to be an undescribed taxon. While investigating the relationship between the Shasta County plants and *V. parvifolium* from coastal California and the Pacific Northwest, we learned of other *V. parvifolium* collections from the Sierra Nevada with dark fruits, even farther disjunct from coastal *V. parvifolium*. We expanded our research to include Sierra Nevada *V. parvifolium* populations, with the goal of determining the relationships among *V. parvifolium* and the putative new taxa in Shasta County and the Sierra Nevada. Our data show morphological, ecological, and genetic distinctions warranting description of two new *Vaccinium* taxa.

TAXONOMIC TREATMENT

Vaccinium shastense J. K. Nelson & L. Lindstrand III, sp. nov. (Fig. 1) "Shasta Huckleberry". ---TYPE: USA, California, Shasta Co., Golinsky Mine, 40°46′11″N, 122°26′32″W; T34N R5W S33 NE¼, ca. 609 m (2,000 ft), 29 August 2012, *L. Lindstrand III s.n.* (holotype: CAS; isotypes: CHSC, DAV, GH, HSC, JEPS, MO, NY, OSC, RSA, STNF, US).

Shrub 0.5–1.7 m, crown-forming or rhizomatous; branches alternate, twigs green and strongly angled, glabrous. Plants erect to decumbent, growing as individual shrubs to rhizomatous thickets or ground covers. Bark of older branches brown to gray, striated. Leaves deciduous, alternate, thin, green and glabrous above, pale below with scattered short hairs, 1.2–4.6 cm long, 0.7–2.7 cm wide, ovate to obovate, base rounded to tapered, tip acute to obtuse, often with mucro; petiole 1 mm; margin entire to occasionally finely serrulate, ciliate with short, forward-pointing, gland-tipped bristles 0.2–0.6 mm long, margin often rolled under and therefore obscuring the ciliate margins. Flowers borne individually in lower axils of new shoots; pedicels recurved, ca. 1 cm long; flowers broadly urceolate, about as

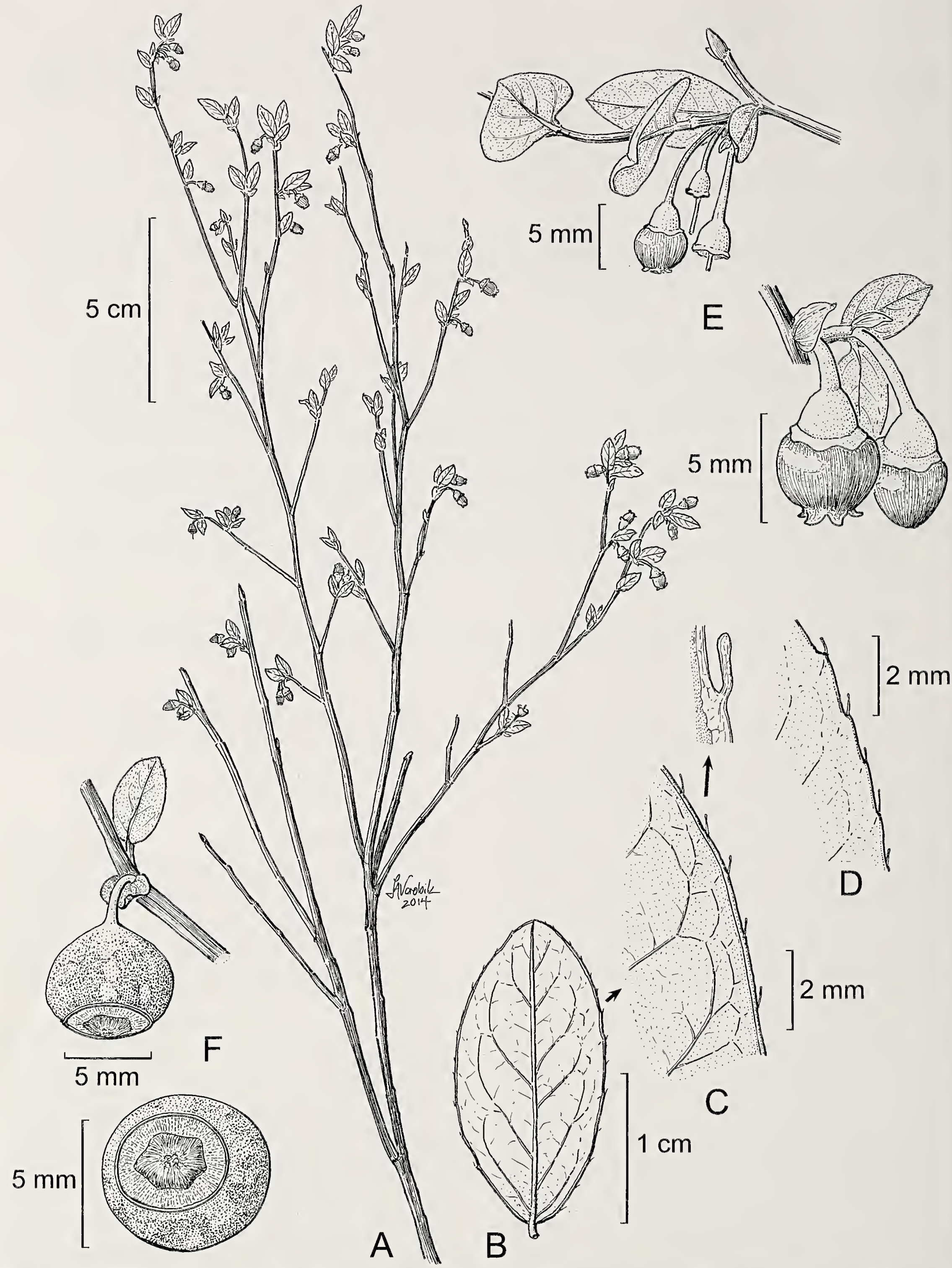

FIG. 1. *Vaccinium shastense.* A. Habit of plant in flower; B. Leaf, adaxial side; Leaf margin, C adaxial, D abaxial, showing forward-pointing marginal cilia; E. Flowers; F. Fruits showing wide hypanthium scar. Drawing by Linda A.Vorobik.

wide as long, with narrow mouth and five short spreading corolla lobes, anthers awned, with tubes longer than the awns. Flowers bright pink to greenish, occasionally whitish, flowering mainly December through June, with occasional flowering after summer rain events, calyx undulate, persisting in fruit as a ring 0.2–1.0 mm long on the distal end of the berry on dry specimens; fruit dark blue, glaucous, 6–8 mm in diameter, with wide persistent calyx ring and hypanthium scar > 3/4 the width of the mature berry; berries quickly deciduous with pedicels still attached. Seeds 1.1–1.2 mm long, 54–108 per fruit, surface pitted.

In addition to different phenotypic and ecological characteristics, *V. shastense* is also genetically distinct from *V. parvifolium*. Recent analysis of microsatellite loci identified high levels of genetic differentiation between *V. shastense* and *V. parvifolium* populations from the coastal regions of northern California, Oregon, and Washington (DeWoody et al. 2012).

Two disjunct *Vaccinium shastense* population groups occur; one in the southeastern Klamath Mountains, California, and one on the western slope of the Sierra Nevada, California. We describe these distinct groups as two subspecies.

Vaccinium shastense subsp. **shastense**

Shrub 0.5–1.7 m. Flowers bright pink to pale pink or greenish, occasionally whitish, flowering December through May. Calyx undulate, persisting in fruit as a ring 0.2–0.5 mm long on the distal end of the berry on dry specimens.

Paratypes: USA, CALIFORNIA. Shasta Co.: Little Backbone Creek, above confluence with Shasta Lake, 40°45′39″N, 122°26′10″W; T34N R5W S33, ca. 335 m (1100 ft), 13 May 2009, *L. Lindstrand III s.n.* (CAS, CHSC, JEPS); Friday-Louden Mine site, along County/USFS Road 5G012, in small tributary to Shoemaker Gulch, 40°45′12″N, 122°27′35″W; T33N R5W S5, ca. 731 m (2400 ft), 18 May 2009, *L. Lindstrand III s.n.* (CAS, HSC, JEPS); Squaw Creek, above confluence with Shasta Lake, 40°44′22″N, 122°28′10″W; T33N R5W S7, ca. 335 m (1100 ft), 27 May 2009, *L. Lindstrand III & H. Kelly s.n.* (CAS, JEPS, STNF); Bully Hill, along a small tributary stream to Horse Creek downstream of a former mine site at Bully Hill, Squaw Creek Arm of Shasta Lake, 40°47′73″N, 122°12′35″W; T34N R3W S21, ca. 335 m (1100 ft), 29 June 2009, *L. Lindstrand III et al. s.n.* (CAS, JEPS); Ingot, in unnamed stream tributary to Little Cow Creek, below Coronado Mine, 40°44′05″N, 122°04′11″W; T33N R2W S11 NW¼, ca. 381 m (1250 ft), 30 April 2014, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF).

Vaccinium shastense subsp. *shastense* most commonly occurs as individual shrubs up to 1.7 m in height (Fig. 2) and occasionally in dense rhizomatous colonies. Older stems tend to die and are replaced by new growth, giving the shrub an abundance of thatch in its interior. The old stems and new growth give the shrub a distinctive broom-like habit, particularly in winter when the stems are leafless. Flowering extends from December through May, with peak flowering in March and April, and opportunistic flowering based on local weather conditions has been observed through September. Plants may flower and fruit more than once during a single growing season; individual shrubs have been observed simultaneously bearing flowers, green fruits, ripe fruits, and overmature dried fruits. Flowers are usually bright pink at anthesis, occasionally paler pink (Fig. 3).

FIG. 2. Typical crown forming shrub habit of *Vaccinium shastense* subsp. *shastense*. Little Backbone Creek, Shasta County, CA. Photo by Len Lindstrand III.

DISTRIBUTION AND HABITAT

Vaccinium shastense subsp. *shastense* occurs in the southeastern Klamath Mountains geomorphic

FIG. 3. Bright pink flowers of *Vaccinium shastense* subsp. *shastense*. South Fork Mountain, Shasta County, CA. Photo by Len Lindstrand III.

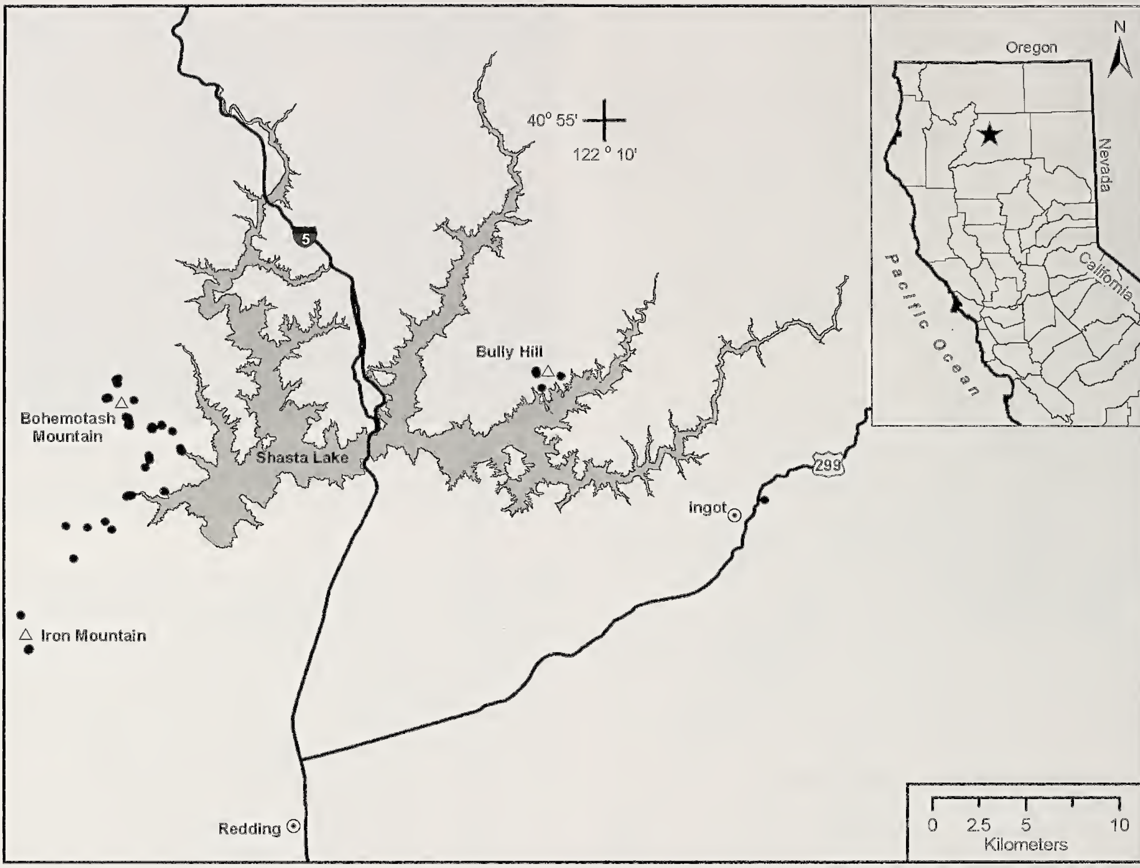

FIG. 4. Distribution of *Vaccinium shastense* subsp. *shastense* (dark circles), southeastern Klamath Mountains, Shasta County, CA.

province (Miles and Goudy 1997) in the vicinity of Shasta Lake, Shasta County, California. This area is characterized by mild, wet winters and hot, dry summers. The average annual precipitation is approximately 156 cm, occurring primarily as rainfall. Average annual temperatures range from 10°C in winter to 32°C in summer. The westernmost population is located at the headwaters of Slickrock Creek, approximately 1 km northwest of Iron Mountain. The easternmost population occurs near Ingot, in the Little Cow Creek watershed approximately 5 km southeast of Shasta Lake. The subspecies range includes three distinct localities: an approximately 46 km^2 area generally southwest of Shasta Lake from the vicinity of Iron Mountain northeast to the southern headwaters of Fall Creek, near Bohemotash Mountain; an approximately 1 km^2 area in the vicinity of Bully Hill on the Squaw Creek Arm of Shasta Lake; and a small area in an unnamed stream tributary to Little Cow Creek in the vicinity of Ingot (Fig. 4).

Vaccinium shastense subsp. *shastense* occurs at elevations between 326–1219 m. All known populations occur in western Shasta County and are located within a region historically known as the Copper Belt of Shasta County, which is divided into two districts; the West and East Shasta Copper-Zinc Districts. The copper deposits are found in acidic lava flows and pyroclastic rocks known from the Devonian Balakala Rhyolite and Triassic Bully Hill Rhyolite geologic units (California Division of Mines and Geology 1974) that occur in this area. Most soils in these areas are acidic residual soils derived from weathering of the parent materials. Additionally, the exposure of sulphide minerals found in these deposits to oxygen and water creates a mild form of sulphuric acid, which circulates through rock and cliff formations, old mine workings, and the surrounding lands, creating acidic water conditions in several local streams and other wetlands. The *V. shastense* subsp. *shastense* populations nearly exclusively occur in areas characterized by these acidic soil and water conditions. At many locations the species grows immediately downstream of historic mine adits and overburden in acidic soil and water. The species also regularly occurs along streams characterized by acid mine discharge water chemistry. Other populations occur as understory shrubs in conifer forests, and in crevices and springs/seeps among rock outcrop or cliff features

FIG. 5. Typical rhizomatous patch habit of *Vaccinium shastense* subsp. *nevadense*. Alpha Road, near Alpha Diggings, Nevada County, CA. Photo by Len Lindstrand III.

characterized by seasonal or perennial acid water chemistry.

The *V. shastense* subsp. *shastense* populations are associated with riparian areas, springs/seeps, and other mesic environments in conifer forest, hardwood-conifer forest, and chaparral habitats. These forest and chaparral habitats are dominated by *Arctostaphylos viscida* Parry, *Cornus nuttallii* Audubon, *Nolithocarpus densiflorus* (Hook. & Arn.) Manos et al. var. *echinoides* (R. Br. ter) Manos et al., *Pinus ponderosa* Lawson & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*, *Quercus chrysolepis* Liebm., *Q. kelloggii* Newb., *Styrax redivivus* (Torr.) L.C. Wheeler, and *Toxicodendron diversilobum* (Torr. & A. Gray) Greene. Species typically associated with *V. shastense* subsp. *shastense* include *Acer macrophyllum* Pursh, *Aruncus dioicus* (Walter) Fernald var. *acuminatus* (Rydb.) H. Hara, *Calycanthus occidentalis* Hook & Arn., *Alnus rhombifolia* Nutt., *Panicum acuminatum* Sw. var. *fasciculatum* (Torr.) Lelong, *Philadelphus lewisii* Pursh, *Polystichum californicum* (D.C. Eaton) Diels, *Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw., *Rhododendron occidentale* (Torr. & A. Gray) A. Gray, *R. columbianum* (Piper) Harmaja, *Rubus armeniacus* Focke, *R. ursinus* Cham. & Schltdl., *Salix lasiandra* Benth. var. *lasiandra*, and *Woodwardia fimbriata* Sm.. Plant taxonomy follows Baldwin et al. (2012).

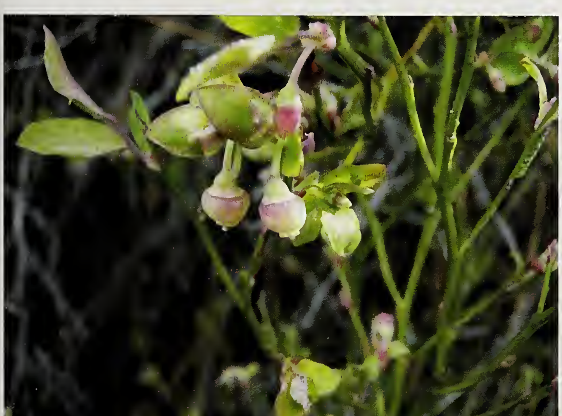

FIG. 6. Greenish to pale pink flowers of *Vaccinium shastense* subsp. *nevadense*. Bean Creek Road, Butte County, CA. Photo by Len Lindstrand III.

Vaccinium shastense subsp. **nevadense** J. K. Nelson & L. Lindstrand III, subsp. nov. "Sierra Huckleberry" --- Type: USA, California, Butte Co., Bean Creek Road, ca 0.8 km north of Little Bald Rock, in an unnamed drainage tributary to Brush Creek, 39°39′43″N, 121°19′29″W; T21N R6E S20 SE¼, ca. 1021 m (3350 ft), 5 June 2013, *L. Lindstrand III s.n.* (holotype: CAS; isotypes: CHSC, DAV, JEPS, STNF).

Shrub 0.5–1.5 m. Flowers pale pink to greenish, occasionally whitish, flowering March through June. Calyx undulate, persisting in fruit as a ring 0.4–1.0 mm long on the distal end of the berry on dry specimens.

Paratypes: USA, CALIFORNIA. El Dorado Co.: Ferrari Mill Road, in a forest drainage, ca. 1.6 km south of Jenkinson Lake, 38°41′58″N, 120°33′58″W; T10N R13E S20 SW¼, ca. 1158 m (3800 ft), 1 July 2013, *J. DeWoody et al. s.n.* (CAS); Rock Creek Road, in a forest drainage at the intersection with USFS road 12N79, ca. 1.8 km west of Bald Mountain Lookout, 38°54′30″N, 120°43′34″W; T13N R12E S11 NW¼, ca. 1036 m (3400 ft), 1 July 2013, *J. DeWoody et al. s.n.* (CAS). Mariposa Co.: Yosemite National Park, Big Creek, about 1 stream mile above the crossing of the Chowchill Mountain Road, westerly side of the stream, 37.50832/-119.66043, T5S R21E S10, ca 4630 ft, 10 July 2009, *D.W. Taylor et al. 20671* (JEPS, YM); Yosemite National Park, tributary headwaters of Moss Creek, north of Big Oak Flat Road and south of Rockefeller Grove Road, on banks of small permanent stream, 250429/-4183389, ca. 1,820 meters (5970 ft), 14 August 2009, *A. Colwell 09-399* (YM). Nevada Co.: Scotts Flat Reservoir, in forest drainage near the intersection of Scotts Flat and Casci Roads, and Scott Flat Campground, 39°17′03″N, 120°55′33″W; T17N R9E S1 NW 1/4, ca. 975 m (3200 ft), 28 June 2013, *L. Lindstrand III & J. DeWoody s.n.* (CAS, CHSC, DAV, JEPS); Alpha Road, on a sericite rock outcropping ca. 0.3 km north of Highway 20, 39°19′35″N, 120°47′09″W; T17N R10E S19 SW¼, ca. 1371 m (4500 ft), 28 June 2013, *L. Lindstrand III & J. DeWoody s.n.* (CAS, JEPS). Plumas Co.: ca. 0.8 km north of Sly Creek Dam, in an unnamed drainage tributary to French Creek ca. 0.8 km northwest of the intersection

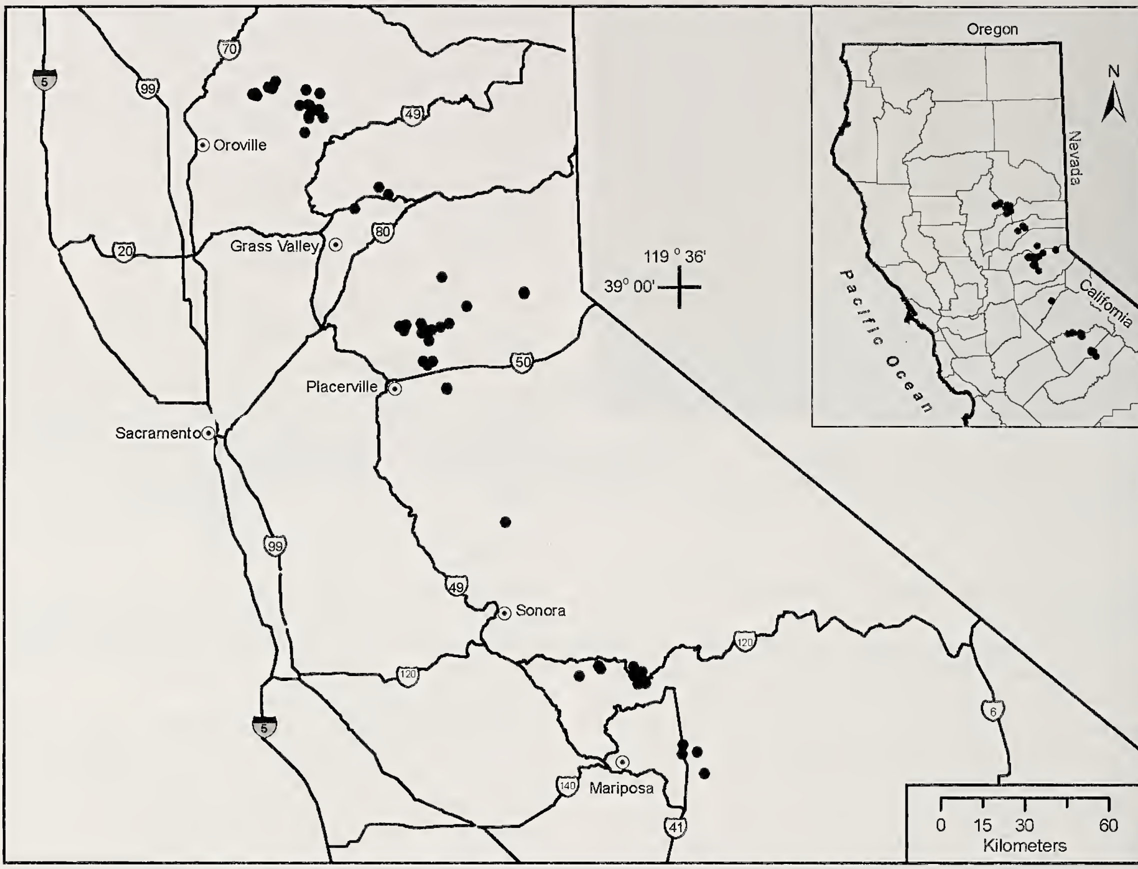

FIG. 7. Distribution of *Vaccinium shastense* subsp. *nevadense* (dark circles), west slope Sierra Nevada, CA.

of USFS roads 21N16 and 21N13, 39°37′15″N, 121°06′24″W; T20N R8E S5 NW¼, ca. 1188 m (3900 ft), 5 June 2013, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF). Tuolumne Co.: Greeley Hill, in vicinity of Red Cloud Mine, south end of Smith Ridge, on gravel USFS road 2.5 miles south of its junction with Moore Creek Road off of the Coulterville Road, in dry shallow gulch near ridgetop, 37.76833/-120.06252, T2S R17E S14 NW1/4 of NE1/4, ca. 1000 m (3280 ft), 28 September 2009, *A. Colwell et al. 09-571* (YM).

Vaccinium shastense subsp. *nevadense* occurs on the western slope of the Sierra Nevada from southeastern Butte County to eastern Madera County, California. The species most commonly occurs in dense rhizomatous colonies (Fig. 5) and occasionally as individual shrubs up to 1.5 m in height. Individuals in most populations have an overall more decumbent habit when compared to those of *V. shastense* subsp. *shastense*. Flowering extends from March to June. *Vaccinium shastense* subsp. *nevadense* also differs from subsp. *shastense* in its greenish to pale pink flowers (Fig. 6) and a longer persistent calyx ring on the fruit (0.5–1.0 mm long on dry specimens).

Besides several slightly different phenotypic characteristics, distinct ecological characteristics and geographic range (see Distribution and Habitat below), *Vaccinium shastense* subsp. *nevadense* is also genetically distinct from *Vaccinium shastense* subsp. *shastense*. Analysis of microsatellite loci showed significant genetic differentiation between the Shasta County and southern Sierra Nevada populations (DeWoody et al. 2012). Subsequent analysis of the same microsatellite loci also showed significant genetic differentiation between the Shasta County and northern Sierra Nevada populations, and found no evidence of a genetic cline between the Shasta Lake and the Sierra Nevada populations (National Forest Genetic Laboratory 2014). The species is absent from the Southern Cascades ecological region, which separates the Shasta County and Sierra Nevada populations.

DISTRIBUTION AND HABITAT

Vaccinium shastense subsp. *nevadense* occurs along the western slope of the Sierra Nevada geomorphic province (Miles and Goudy 1997) from the vicinity of Bald Rock, Butte County,

FIG. 8. Red, translucent fruit of *Vaccinium parvifolium* and narrow hypanthium scar. Photo by T. Abe Lloyd, courtesy of Salal, the Cascadian Food Institute.

FIG. 9. Dark blue to purple, glaucous fruit of *Vaccinium shastense* and wide hypanthium scar. Golinsky Mine, Shasta County, CA. Photo by Len Lindstrand III.

California, south to Fresno Grove Big Trees, Madera County, California (Fig. 7). The north-south extent of its range is approximately 360 km and includes ten Sierra Nevada counties. The species occurs on various sedimentary, igneous, and metamorphic substrates including Mesozoic granitic rocks, Paleozoic marine rocks, Tertiary volcanic flow andesite rocks, and undivided pre-Cenozoic metavolcanic rocks (Jennings et al. 1977). Known populations occur at elevations between approximately 609–2011 m. The species is found in locations characterized by 89 to 200 cm of annual precipitation, which occurs as rainfall and snow, and many populations occur in areas subject to persistent snow.

Vaccinium shastense subsp. *nevadense* occurs as an understory shrub in low- to mid-elevation mixed conifer forests, and is occasionally found in disturbed locations such as road cuts and former mine sites. Habitats at known populations include mesic and shady draws, springs/seeps, meadow edges, riparian areas, and rock outcroppings. Species composition in these mixed conifer forest habitats varies by location and includes *Abies concolor* (Gordon & Glend.) Hildebr., *Arbutus menziesii* Pursh, *Arctostaphylos manzanit*a Parry subsp. *manzanita*, *A. viscida*, *Calocedrus decurrens* (Torr.) Florin, *Ceanothus cuneatus* Nutt. var. *cuneatus*, *Chrysolepis sempervirens* (Kellogg) Hjelmq., *Cornus nuttallii*, *Corylus cornuta* Marshall subsp. *californica* (A. DC.) E. Murray, *Notholithocarpus densiflorus* var. *echinoides*, *N. densiflorus* var. *densiflorus*, *Pinus lambertiana* Douglas, *P. ponderosa*, *Pseudotsuga menziesii* var. *menziesii*, *Quercus chrysolepis*, *Q. kelloggii*, and *Taxus brevifolia* Nutt. Species typically associated with *V. shastense* subsp. *nevadense* include *Adenocaulon bicolor* Hook., *Alnus rhombifolia*, *Amelanchier alnifolia* (Nutt.) M. Roem. var. *semiintegrifolia* (Hook.) C.L. Hitchc., *Chimaphila umbellata* (L.) W.P.C. Barton, *Equisetum arvense* L., *Fragaria virginiana* Mill., *Frangula purshiana* (DC.) J.G. Cooper subsp. *annonifolia* (Greene) Sawyer & S.W. Edwards, *Goodyera oblongifolia* Raf., *Holodiscus discolor* (Pursh) Maxim, *Leucothoe davisiae* A. Gray, *Physocarpus capitatus* (Pursh) Kuntze, *Pteridium aquilinum* var. *pubescens*, *Rhododendron columbianum*, *R. occidentale*, *Rubus parviflorus* Nutt., *Sorbus scopulina* Greene, and *Symphoricarpos mollis* Nutt.

IDENTIFICATION AND TAXONOMIC RELATIONSHIPS

Vaccinium shastense strongly resembles *V. parvifolium* superficially in its deciduous habit, green angled twigs, and number and placement of flowers. The most obvious difference between *V. parvifolium* and *V. shastense* is in fruit color and hypanthium scar dimensions; *V. parvifolium* has red translucent berries without surface waxy bloom (hence the common name red huckleberry) with a narrow hypanthium scar (Fig. 8), whereas

FIG. 10. Fallen *Vaccinium shastense* subsp. *shastense* fruit with pedicels attached. Golinsky Mine, Shasta County, CA. Photo by Julie Kierstead Nelson.

FIG. 11. Pitted seed surface of *Vaccinium shastense*. Photo by Martin Lenz.

V. shastense has dark blue to purple, glaucous fruits with a wide hypanthium scar (Fig. 9). Berries of both subspecies of *V. shastense* drop quickly after ripening, with pedicels still attached (Fig. 10), unlike those of *Vaccinium parvifolium*, which tend to persist on the shrub for at least two months (Vander Kloet 1988). *Vaccinium shastense* also has a pitted seed surface (Fig. 11) compared to the lengthwise striations found on *V. parvifolium* seeds (Fig. 12). Differentiating between the species in fruit is not challenging. Fortunately, there is also a consistent vegetative feature distinguishing the two species; namely, the leaf margin character. *Vaccinium parvifolium* leaves typically lack marginal cilia, whereas *V. shastense* leaves consistently have distinctive, forward-pointing multicellular marginal cilia (Figs. 1B, C, D; 13, 14). When present on *V. parvifolium*, the marginal cilia are confined to the lower third of the leaf margin and are 0.1–0.14 mm in length, whereas *V. shastense* leaves have marginal cilia

FIG. 12. Lengthwise striations on seed surface of *Vaccinium parvifolium*. Photo by Steve Hurst,, hosted by the USDA-NRCS PLANTS Database, http://plants.usda.gov/core/profile?symbol=VAPA.

FIG. 13. Leaf margin of *Vaccinium shastense*. Photo by Martin Lenz.

that are 0.2–0.6 mm long (P. Fritsch, personal communication). *Vaccinium parvifolium* occasionally has strongly serrate leave margins, with teeth that may or may not be bristle-tipped. This strongly serrate leaf form has not been seen in either subspecies of *V. shastense*. Unlike *V. parvifolium*, which often grows on stumps and logs (Hitchcock and Cronquist 1973), *V. shastense* is confined to soil or occasionally rock crevices.

The third California species with strongly angled, green twigs is *V. scoparium* Leiberg ex Coville, a diminutive plant with serrate leaves (*V. shastense* leaves are entire), tiny flowers (<4 mm long, compared to 1 cm for *V. shastense*) and smaller red berries (3–6 mm diameter, compared to 6–8 mm blue berries for *V. shastense*). The anthers of *V. shastense* are awned (Fig. 15), as are those of *V. parvifolium* and *V. scoparium*.

Vaccinium parvifolium and *V. shastense* do not appear to be sympatric, as *V. parvifolium* is restricted to the coastally influenced regions of California and the more mesic parts of the western and high Klamath Mountains of Siskiyou County, extending northward, west of the Cascade Crest, through Oregon and Washington to British Columbia and Alaska. *Vaccinium*

FIG. 14. Marginal cilium of *Vaccinium shastense* leaf. Photo by Martin Lenz.

FIG. 15. Awned anthers of *Vaccinium shastense*. Photo by Martin Lenz.

shastense is a species of inland California, from the southeastern Klamath Mountains and Sierra Nevada; these are areas with hot summers and absent coastal climate influences. *Vaccinium shastense* is endemic to California and plants with the overall habit of this and *V. parvifolium* can safely be determined by geographic location alone. The combination of vegetative and fruiting characteristics and distinct geographic ranges make identification of *V. parvifolium*, *V. shastense* subsp. *shastense*, and *V. shastense* subsp. *nevadense* straightforward.

In California, *V. scoparium* is restricted to the Klamath and Cascade Mountains of Del Norte, Humboldt, Siskiyou and Trinity Counties, where it grows in montane conifer forests. The species has been not been collected from Shasta County or the Sierra Nevada. *Vaccinium scoparium* and *V. shastense* are not sympatric.

Vaccinium shastense subsp. *shastense* differs from *V. shastense* subsp. *nevadense* in more subtle characters of growth habit, flower color, and length of persistent calyx ring on the fruit (see key below). The two subspecies of *V. shastense* are also genetically distinct, and disjunct, with the southern Cascade Range of California lying between the southeastern Klamath Mountains distribution of *V. shastense* subsp. *shastense* and the Sierra Nevada distribution of *V. shastense* subsp. *nevadense* (Fig. 16). Thus, the subspecies identification can also be determined by geographic location, absent other characters.

HISTORY OF *VACCINIUM SHASTENSE* COLLECTIONS

Vaccinium shastense subsp. *shastense* was first collected on April 30, 1900 near the Afterthought Mine (present day Ingot location, northeast of Redding) by Milo Baker, who wrote in his field book: "A small bush with the appearance of a huckleberry, yet from my recollections of the bush, this is different. This however is only an impression." (Book C, Milo S. Baker papers).

A second collection was made by James McMurphy on June 10, 1914 from "hill above mine, Kennet." Kennett was a town and the location of a copper smelter that processed ore from the many mines around what is now Shasta Lake; Kennett itself lies under the lake's waters now, not far from Shasta Dam. These collections represent the only two made before the first author discovered the plant growing at Golinsky Mine, on the west side of Shasta Lake, on June 7, 1991.

Vaccinium shastense subsp. *nevadense* is a different story, having been collected repeatedly up and down the Sierra Nevada for over a hundred and twenty years. J. W. Congdon collected the first specimens in 1893 from Mariposa County, and that same year by A. M. Carpenter from Nevada County. Specimens were collected over the years by many famous twentieth-century California botanists: John Thomas Howell, Enid Michael, Lewis S. Rose, G. Thomas Robbins, W. L. Jepson, and L. R. Heckard. Plants from the northern Sierra Nevada counties of Butte (1966), Plumas (1975), and Yuba (1994), were documented later than those of the central Sierra Nevada. Gehrung (2001) made note of these plants in her thesis on section *Myrtillus* in northern California, where she described plants from Plumas National Forest as anomalous *V. parvifolium* that were rhizomatous, with blue berries, and "pedicels that come off with the berries when picked" (pg. 60).

The "blue-berried red huckleberry" would have remained an unexplored curiosity but for a 2003 proposal by the U. S. Bureau of Reclamation to enlarge Shasta Lake by raising Shasta Dam, leading to intensive field surveys, discovery of additional *Vaccinium* populations west of Shasta Lake, and funds to investigate the genetic relationship of these plants to red-fruited typical *V. parvifolium*. Alison Colwell of Yosemite National Park made several collections of blue-berried, decumbent plants from Tuolumne County, and brought them to our attention in 2009; at that point we broadened our study of anomalous blue berried *V. parvifolium* beyond Shasta County to encompass the Sierra Nevada plants.

RARITY AND CONSERVATION STATUS

Vaccinium shastense subsp. *shastense* is endemic to the southeastern Klamath Mountains in the general vicinity of Shasta Lake, Shasta County, California. The species is known from more than 20 occurrences at 14 general locations (Fig. 4), ranging from several isolated plants to 1000+ plants occurring over large areas. *Vaccinium shastense* subsp. *shastense* appears to have specific ecological microhabitat requirements related to acidic edaphic and water conditions. Habitat is restricted to locations where natural geologic characteristics or historic mining disturbances provide these acidic conditions and

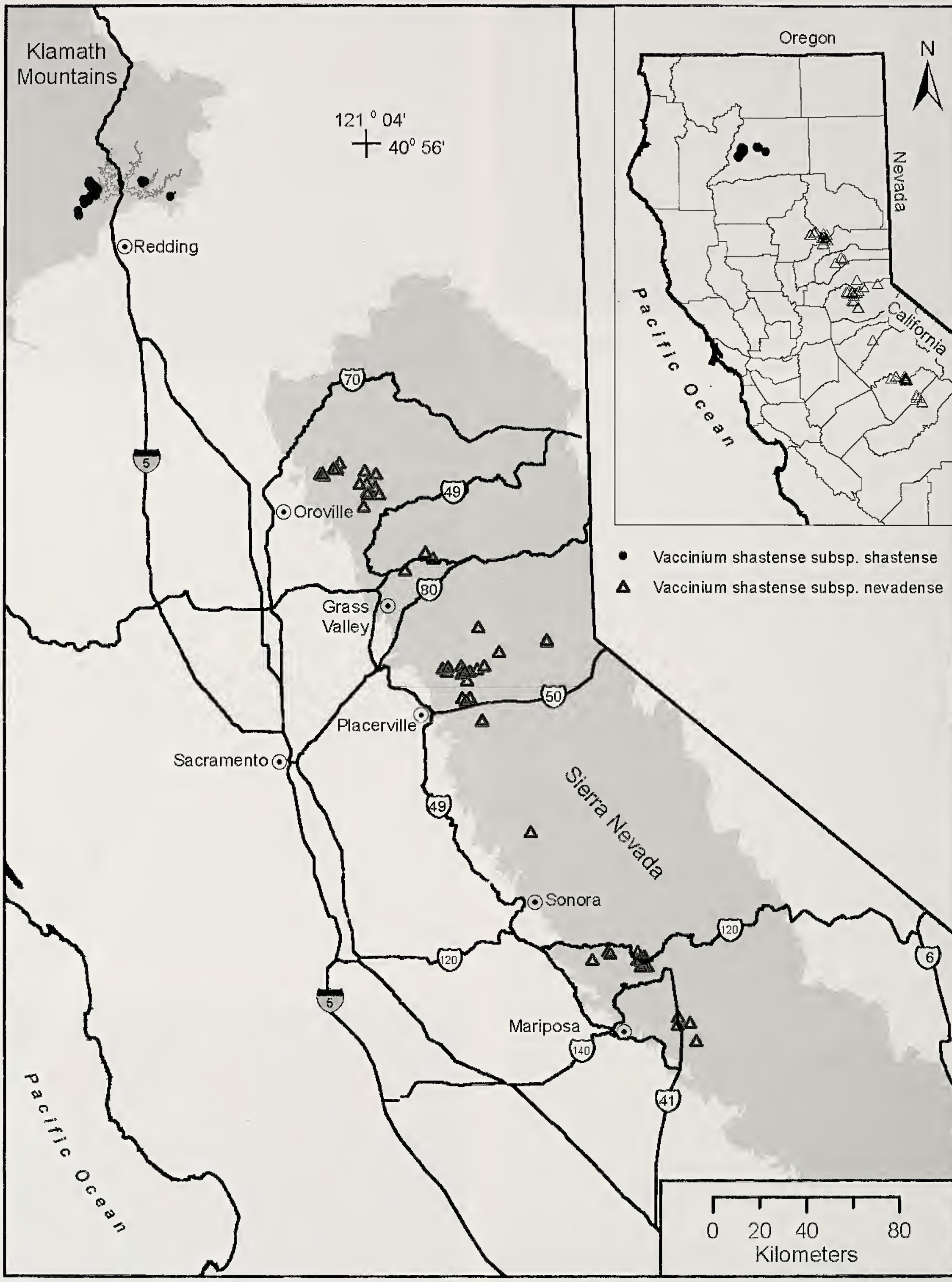

FIG. 16. Southeastern Klamath Mountain distribution of *Vaccinium shastense* subsp. *shastense* and Sierra Nevada distribution of *Vaccinium shastense* subsp. *nevadense*, California. Ecological unit boundaries from Miles and Goudy (1997).

adequate soil moisture. Specifically, *V. shastense* subsp. *shastense* populations are directly correlated to habitats with geologic characteristics causing naturally occurring acidic conditions, or former copper mine sites and adjacent areas affected by those activities where acidic conditions occur and have been exacerbated. *Vaccinium shastense* subsp. *shastense* does not occur in similar habitats not influenced by either naturally occurring acidic conditions or the mining activities that have produced these acidic conditions.

Many of the *V. shastense* subsp. *shastense* localities are disturbed habitats, including roadside ditches and road-cuts, overburden from mine adits, drainages and eroded slopes, riparian zones in streams characterized by acid mine discharge water chemistry, and forested slopes in areas formerly denuded of vegetation due to copper smelting during the early 1900s. Undisturbed localities include rock outcrop and cliff formations, and forested slopes and drainages. The species is adapted to survive fire, as basal sprouting and rhizomatous spreading have been observed by the second author in individuals and populations subjected to wildfire. *Vaccinium shastense* subsp. *shastense* could be useful for mine reclamation on moist, acidic sites within its narrow geographic range.

Vaccinium shastense subsp. *shastense* is rare in terms of its number of known populations and narrow geographic distribution; however, based on the distribution, size, and remoteness of most populations, their resilience to a variety of disturbances, and the type and level of known or potential threats, the species is not presently endangered or threatened. The species is, however, narrowly endemic and uncommon such that its status should be monitored. We recommend that *V. shastense* subsp. *shastense* be considered for a California Rare Plant Rank of 1B.3 (Plants Rare or Endangered in California and elsewhere; not very threatened in California (<20% of occurrences threatened/low degree and immediacy of threat or no current threats known) in the California Department of Fish and Wildlife (CDFW) Special Vascular Plants, Bryophytes, and Lichens list (CDFW 2014) and the California Native Plant Society's (CNPS) Inventory of Rare and Endangered Vascular Plants of California (CNPS 2001, 2014).

Vaccinium shastense subsp. *nevadense* occurs along the western slope of the Sierra Nevada. The species north-south range extends approximately 360 km across ten counties. Although somewhat uncommon and irregularly distributed, the species is known from over 100 occurrences and appears fairly widespread across its range (Fig. 7). Most known occurrences are located in remote or fairly remote forest areas, including National Forest, California State Forest, and National Park lands. Given the number and locations of known populations, size of the species range, and the type and level of known or potential threats, recommendation of any regulatory status or conservation rank for *Vaccinium shastense* subsp. *nevadense* does not appear warranted.

Key to California *Vaccinium*, with *V. shastense* Taxa Included

Key to *Vaccinium* from Baldwin et al. (2012), modified to add *V. shastense* and subspecies.

1. Leaves evergreen, leathery, veins not prominent abaxially; pedicel jointed to flower; filaments ± hairy
  2. Plant <1.5 dm, branches slender; leaf generally 7–17 mm, ± entire; corolla lobes >> tube, reflexed when anthers open . . . . *V. macrocarpon* Aiton
  2′ Plant 5–30 dm, branches stout; leaf 20–50 mm, serrate; corolla lobes < tube, erect to spreading when anthers open . . . . *V. ovatum* Pursh

1′. Leaves deciduous (rarely evergreen in young plants of *V. parvifolium*), thin or ± thick, veins generally prominent abaxially; pedicel not jointed to flower; filaments glabrous
  3. Leaf entire; calyx lobes generally > tube, persistent; twigs not angled, not green; flowers 1–4 on leafless older shoots . . . . *V. uliginosum* L. subsp. *occidentale* (A. Gray) H. Hara
  3′ Leaf serrate or minutely so, or ciliate (but see *V. parvifolium*); calyx lobes ± 0 or generally <tube, deciduous; twigs angled or not, green or not; flowers often 1 in axils of lowest leaves of youngest shoots
    4. Twigs strongly angled, green; fruit red to dark blue or purple
      5. Leaves ciliate with forward-pointing bristles 0.2–0.6 mm long, margins inrolled; otherwise entire or barely serrate; fruits dark blue, glaucous; hypanthium scar >3/4 width of berry
        6. Persistent calyx ring on berry 0.2–0.5 mm long on dry specimens, growth habit generally erect, occasionally rhizomatous, often crown forming shrubs 5–17 dm tall; flowers bright pink to pale pink; western Shasta County. . . . . subsp. *shastense*
        6. Persistent calyx ring on berry 0.4–1.0 mm long on dry specimens, growth habit generally decumbent, occasionally upright, often rhizomatous, forming ground cover, occasionally crown forming shrubs 2–15 dm tall; flowers pale pink to greenish; west slope Sierra Nevada . . . . subsp. *nevadense*

5′ Leaves not ciliate or occasionally ciliate on lower third, cilia if present 0.1–0.14 mm long; fruits red, translucent, not glaucous; hypanthium scar up to 1/2 the width of berry.

7. Plant erect shrub, 10–40 dm, generally not rhizomed; leaf entire to serrate or with only deciduous, with mucro, abaxially (especially midvein) puberulent . . . . *V. parvifolium*

7′ Plant brushy shrub, <5 dm, rhizomed; leaf serrate, abaxially glabrous . . . . *V. scoparium*

4′ Twigs not or weakly angled, ± green or yellow-green but not green; fruit not red (rarely dark red in *V. membranaceum* Douglas ex Torr.)

8. Plant generally 5–15 dm; twigs weakly angled; leaf generally ovate to elliptic or obovate, 2–5 cm, thin, membranous, base often rounded to truncate, tip acute . . . . *V. membranaceum*

8′ Plant generally <5 dm; twigs not or weakly angled; leaf generally oblong or elliptic to obovate or oblanceolate, rarely elliptic, generally 1–3.5 cm, generally thin but not membranous, base tapered, tip seldom acute

9. Youngest twigs generally puberulent or glandular; leaf not glaucous, generally oblong or obovate to elliptic; corolla narrowly urn-shaped; fruit <9 mm wide . . . . *V. cespitosum* Michx.

9′ Youngest twigs generally glabrous, glaucous; leaf glaucous, obovate to oblanceolate (elliptic); corolla ± spheric; fruit > 9 mm wide . . . *V. deliciosum* Piper

Acknowledgments

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Appendix

Additional Specimens Examined

Vaccinium shastense subsp. **shastense**

USA. CALIFORNIA. Shasta Co.: Cow Creek Canyon, 1 May 1900, M. S. Baker (UC); Hill above mine, Kennett, 10 June 1914, *J. McMurphy, s.n.* (DS); West side Shasta Lake (Golinsky Mine), Shasta-Trinity National Forests, Shasta Lake Ranger District, 7 June 1991, *J. K. Nelson 91-63* (JEPS); North Fork Little Backbone Creek, 1/4 mile west of Golinsky Mine, growing on creek edge in full sun, T34N R5W S28, 1 May 1992, *J. K. Nelson 92009* (RSA); Friday-Louden Mine adit along County Road 5G12 to Bohemotash Mountain from Shasta Dam, west side of Shasta Lake, ca 20 miles NW of Redding, T33N R5W S5, 13 April 2004, *J. K. Nelson 2004-012* (CAS); Bully Hill Mine, north side of Shasta Lake at confluence of Squaw Creek and Pit River arms, small population in depression below mine road east of Town Creek, T34N R3W S15, 8 September 2006, *J. K. Nelson & L. Lindstrand III 2006-045* (CHSC, JEPS); Golinsky Mine, along dry slopes, wet seeps, and seasonal drainages on slopes below former Golinsky Mine site, Little Backbone Creek, Shasta Lake, T34N R5W S28, 11 May 2009, *L. Lindstrand III s.n.* (CAS, CHSC, JEPS); Little Backbone Creek watershed, Golinsky Mine, T34N R5W S28, 28 June 2011, *J. K. Nelson et al. 2011-33* (CHSC); Friday Louden mine adit, adjacent to County Road 5GO12, west slope of Shasta Lake, ca 2 mi NW of Shasta Lake, 8 July 2011, *J. K. Nelson & T. Derksen 2011-035* (CAS, CHSC, DAV, HSC, JEPS, STNF); Northwest of Bohemotash Mountain, along unnamed headwater stream tributary to Fall Creek, T34N R5W S19, 21 September 2011, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF); Southwest slope of Bully Hill, along stream and below old copper mine workings, T34N R3W S16, 17 October 2012, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF); West of Bohemotash Mountain, on forested slope above unnamed headwater stream tributary to North Fork Squaw Creek, T34N R5W S19 SW¼, ca. 1158 m (3800 ft), 10 October 2012, *L. Lindstrand III & J. K. Nelson s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF); Whiskeytown-Shasta Trinity National Recreation Area, along forest road 35N05 (Westside Road) at Friday Louden Mine adit, along a tributary stream of Shoemaker Gulch above Shasta Lake, T33N R5W S5, 18 June 2012, P. Fritsch et al. s.n. (CAS); Northwest of Bohemotash Mountain, along unnamed headwater stream tributary to Fall Creek, T34N R5W S19, 26 April 2013, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, JEPS, STNF); Ingot, in unnamed stream tributary to Little Cow Creek, below Coronado Mine, T33N R2W S11 NW¼, 5 September 2014, *L. Lindstrand III & J. K. Nelson s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF); Northwest slope of Iron Mountain, in draw at the headwaters of Slickrock Creek, T 33N R 6W S28SE¼, 26 September 2014, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF).

Vaccinium shastense subsp. **nevadense**

USA. CALIFORNIA. Butte Co.: Crossing of Lewis Creek with Lewis Creek Ridge Road, NW of Sly Creek Reservoir, 29 June 1966, *C. R. Quick 66-34* (CAS); NE of Oroville at Little Bald Rock, T21N R6E S20, 14 June 1980, *R. A. Schlising 3708* (CHSC); Swamp, where the road forks and crosses French Creek Reservoir, 15 September 1981, *L. Ahart 3170* (CHSC, CAS); Along Bean Creek Road ca 4/5 mile east of Little Bald Rock, T21N R6E S29, 24 May 1983, *J. D. Jokerst et al. 1778* (CHSC); Along dirt road 2 miles south of Milsap Bar, about 23 miles northeast of Oroville, 29 July 1983, *L. Ahart 4221* (CHSC, CAS); Plumas National Forest, near Little Bald Rock, T21N R6E S20, 26 May 1987, *L. Hanson 299* (CHSC); Ca 0.4 mi NW of Little Bald Rock, 0.2 mi E of Bald Rock Rd., T21N R6E S20, 26 April 1990, *B. Castro 427* (CHSC); Northern high Sierra Nevada, narrow northeast-trending ridge overlooking South Branch Middle Fork Feather River, about 1.7 mi east of Milsap Bar, T21N R7E S7, 27 July 1994, *L. P. Janeway 4701* (CHSC); Watson Ridge, about 3 mi northeast of Bald Rock Dome, T21N R6E S13, 8 May 1995, *L. P. Janeway 4762* (CHSC, CAS); Watson Ridge on both sides of USFS Rd. 21N25A, T21N R6E S13, 16 October 1996, L. Gehrung 123 (CHSC); Northern high Sierra Nevada, along Bean Creek Road 1.1 km east of Bald Rock Road, T21N R6E S20, 25 May 2010, *L. P. Janeway 92980* (CHSC); 0.5 air miles northeast of Little Bald Rock, northeast of and below Bean Creek Road, 0.6 miles from Bald Rock Road, 5 August 2011, *P. Zika et al. 25710* (CAS); Bean Creek Road, ca 0.5 mi. north of Little Bald Rock, in an unnamed drainage tributary to Brush Creek, 2 April 2013, *L. Lindstrand III s.n.* (CAS, JEPS). Calaveras Co.: San Antonio Creek, 6 August 1906, *W. R. Dudley s.n.* (CAS); Trail to San Antonio Falls Calaveras, 17 June 1912, *H. A. Walker 2738* (UC); 2 ½ miles east northeast of Creighton, Big Trees (Calaveras), 25 October 1935, *W.R. Howden s.n.* (UC). El Dorado Co.: Rock Creek El Dorado National Forest, T12N R11E S15, 13 May 1915, *O. M. Evans* (JEPS); Rubicon Springs, Tahoe region, 8 July 1922, H. M. Mitchell s.n. (CAS); 1 mi. west of Blair Saw Mill, El Dorado National Forest, 6 July 1934, *P.L. Johannsen 369* (UC); 0.25 mi south of Bob's Cabin, El Dorado National Forest, Pyramid Peak Quad., T13N R13E S24, 9 October 1934, *P. L. Johannsen 510* (UC); Along borders of Long Creek, 1–2 mi. from its confluence with South Fork American River, 28 May 1944, *G. T. Robbins 1639* (CAS, UC); Along north shore of Rockbound Lake, Rockbound Valley, Desolation Valley Wilderness Area, T11N R12E S20-21, 5 August 1945, *G. T. Robbins 2083* (CAS, UC); Watershed of Little Silver Creek, a tributary of Rock Creek on the south side of Georgetown Divide about 1/2 mile below summit, T13N R11E S9, 25 April 1960, *R. E. Rockey 1* (CAS, JEPS, UC); About 7 mi east of Georgetown (along Pilot Creek, nw of Blodgett Forest headquarters), Pilot Creek, 30 May 1969, *L. R. Heckard 2244* (JEPS); Blodgett Experimental Forest, 27 May 1970, *J. T. Howell & G.H. True 46529* (CAS); Blodgett Forest, 27 May 1970, *L. Rose 70044* (CAS); Blodgett Forest, 19 July 1973, *J. T. Howell & P. Rubtzoff s.n.* (CAS); Blodgett Forest: Chinquapin Flat Road ca. 1.6 mi. south of Gaddis Creek Road; ca. 175 yards down the southwest slope from road (Comp. 600R), forest floor ca. 75 yards up the slope from South Blodgett Road, 19 May 1976, *P. Rubtzoff 8539* (CAS); Blodgett Forest: headquarters area (Comp. 250R), forest floor between Staff House and Bunkhouse, 19 May 1976, *P. Rubtzoff 8543* (CAS); Slab Creek; ca. 1 air mile S of Pino Grande (site), eastern vicinity Blodgett Forest, T21N R12E S28, 21 June 2006, *D. W. Taylor 19551* (JEPS). Madera Co.: Trail from Fresno Big Trees 13 July 1901, *W. R. Dudley s.n.* (CAS) (labeled as Fresno Co.); Fresno Grove Big Trees,

6 August 1931, *W. L. Jepson 15972* (UC). Mariposa Co.: Red Cloud, 31 May 1893, *J. W. Congdon s.n.* (CAS, DS); Red Cloud, 1 June 1895, *J. W. Congdon s.n.* (UC); Near Wawona, 26 May 1924, *J. T. Howell 353* (CAS); Merced Grove of Big Trees, 4 May 1934, *E. Michael s.n.* (CAS); Bean Creek, along Dogtown Road, at southernmost creek ford, 20 March 1977, *D. W. Taylor 15924* (JEPS); Merced Grove where the road crosses Moss Creek just inside the park boundary, 28 June 2004, *A. Colwell & C. Coulter AC 4-106* (UC); Yosemite National Park; old logging road south of Crane Flat campground, 30 June 2005, *A. Colwell et al. AC 5-39* (UC); Yosemite National Park.; Unnamed drainage west of Crane Flat Campground about one mile from park boundary, 19 June 2007, *D. Grossenbacher & L. Dennis 510* (UC); Tributary of Moss Creek south of Big Oak Flat Road, one km south southeast of Crane Flat Lookout, 26 June 2007, *A. Colwell et al. Jul-78* (UC); Tributary headwaters of Moss Creek between Big Oak Flat Road and Rockefeller Grove Road, VAPA10-6 and LEDA10-6 plots, v 2.6 meters, 7 August 2007, *A. Colwell 07-297* (UC). Nevada Co.: Along road at Scotts Flat L., 1 June (year unknown), *L. S. Mott LM6717* (CAS); Nevada County, September 1893, *A. M. Carpenter s.n.* (UC); Nevada County, September 1893, *A. M. Carpenter s.n.* (UC); Alpha Road just north of Highway 20, 13 miles east of Nevada City, 23 August 1965, *G. H. True & J. T. Howell 2446* (CAS); Scotts Flat Reservoir on Deer Creek about 5 miles east of Nevada City, 25 August 1965, *G. H. True & J. T. Howell 2538* (CAS); Skillman Flat on Washington Ridge, ca. 12 mi. E. of Nevada City, 28 May 1970, *J. T. Howell & G. H. True 5357* (CAS); South Fork of Yuba River ca. 1 mi. below Washington, 24 May 1971, *G. H. True & J. T. Howell 6591* (CAS); Booth Point, 1 mi. north thereof, southerly rim Middle Yuba River Canyon, 29 July 2005, *D. W. Taylor & T. Engstrom 19442* (JEPS); South Fork of Yuba River below Washington, 27 June 2013, *L. Lindstrand III s.n.* (CAS, JEPS). Placer Co.: Sugar Pine Tahoe National Forest, 16 May 1931, *L. S. Smith 2452* (UC). Plumas Co.: Along Lost Creek, about 6 miles north of the Sly Creek Dam, 2 July 1975, *L. Ahart 837* (CHSC, CAS); on French Creek, tributary to Sly Creek Reservoir, S side of USFS Rd. 21N16, T20N R8E S5, 1 September 1997, *L. Gehrung 158* (UC); on French Creek, tributary to Sly Creek Reservoir, N side of USFS Rd. 21N16, T20N R8E S5, 1 September 1997, *L. Gehrung 157* (UC). Tuolumne Co.: North Crane Creek Yosemite National Park, Yosemite Quad., T2S R20E S7, 21 June 1935, *W. B. Augustine 155* (UC); 1 mi. NW Park Lookout; Stanislaus National Forest, Yosemite Quad., T2S R19E S13, 16 August 1935, *C. M. Belshaw 64A* (UC); Stanislaus River bridge near Twain Harte - Sierra Nevada, T2S R18E S4NE¼, 4 June 1954, *J. T. Howell 29924* (CAS); South Fork Stanislaus River - Sierra Nevada, 5 June 1955, *J. T Howell 30278* (CAS); In drainage cresting Pilot Ridge Sierra Nevada, Pilot Ridge, 8 July 1982, *D. W. Taylor 8021* (JEPS); Above FS road 1S13, lower slopes of Pilot Ridge, South Fork Tuolumne River drainage, Stanislaus National Forest - Sierra Nevada, 27 April 1996, *J. R. Shevock 13280* (CAS); North Crane Creek, 26 May 2004, *A. Colwell & A. Sanders AC 4-10* (UC); North Crane Creek, 30 August 2004, *A. Colwell & A. Sanders AC 4-129* (UC); Yosemite National Park, Rockefeller Grove Road, 400 m N of Big Oak Flat Road, 13 July 2005, *A. Colwell et al. AC 5-71* (UC); Yuba Co.: On the south side of Schwartz Meadow, on the east side of La Porte Road, about 4 miles northeast of Strawberry Valley, T20N R8E S10, 27 June 1994, *L. Ahart 7399* (CHSC, JEPS); ca 2 air miles E of Clipper Mills and ca 1.6 mi. NE of Big Hill, along USFS RD 20N04, on ridge between Hampshire and Missouri Creeks, T19N R8E S6, 23 April 1997, *B. Castro 724* (CHSC). Unknown Co.: Tahoe Forest, 1 June 1913, *G. M. Noyes 198* (CAS).

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NOTEWORTHY COLLECTION

ARIZONA

ECHINOCEREUS CHLORANTHUS Haage subsp. *RHYOLITHENSIS* W. Blum & Mich. Lange (CACTACEAE). — Greenlee County, Big Lue Mountains, 33.1097°, -109.0681° (WGS84), 1,735 m (5,692 ft) elevation, along Coal Creek, 1.9 km west of the New Mexico state line, 22 km ENE of Clifton, 26 January 2014, *M.A. Baker 17873.5 with M.A. Cloud-Hughes* (ASU 289472!). Thirty individuals found within ca. 10 ha, mainly on northeast facing hillsides of rhyolite and basalt in *Pinus ponderosa* P. Lawson & C. Lawson woodland with *Agave parryi* Engelm., *Aristida purpurea* Nutt., *Bouteloua curtipendula* (Michx.) Torr., *B. gracilis* (Kunth) Lag. ex Griffiths, *Cercocarpus montanus* Raf., *Cylindropuntia spinosior* (Engelm.) F.M. Knuth, *Garrya wrightii* Torr., *Juniperus deppeana* Steud., *Muhlenbergia longiligula* Hitchc., *Opuntia phaeacantha* Engelm., *Pinus cembroides* Zucc., *Prunus virginiana* L., *Quercus emoryi* Torr., *Q. grisea* Liebm., *Schizachyrium scoparium* (Michx.) Nash, and *Yucca baccata* Torr.

A chromosome determination of $n = 11$ was made during meiosis of microgametogenesis by M.A. Baker from the same individual and voucher listed above.

Previous knowledge. Blum and Lange (1998) circumscribed populations in New Mexico having five or more central spines, generally reddish spines, and brown flowers as *Echinocereus chloranthus* subsp. *rhyolithensis*. The holotype specimen of *Echinocereus chloranthus* subsp. *rhyolithensis* was collected by Pierce in Lake Valley, Sierra County, New Mexico in 1961 (UNM 25336!).

Blum et al. (2012) listed *Echinocereus chloranthus* subsp. *rhyolithensis* as being present in Arizona based on information from David Ferguson. However, they were unable to locate Arizona sites. A report with photographs of this taxon from the Big Lue Mountains in Arizona was posted to the online forum CactiGuide by a user named Preston Sands in December 2008 (CactiGuide.com 2008–2009). Peter Breslin located plants in the fall of 2013. Böhm and Böhm published observations of *Echinocereus chloranthus* subsp. *rhyolithensis* in Arizona near this locality in 2013; however, that publication did not include specific locality data or a voucher specimen. Another population of this taxon was recently found from the Blue Range Primitive Area of Apache-Sitgreaves National Forest, Arizona, and photographically documented by Owen Lorentzen of Pleasanton, New Mexico.

The holotype for *Echinocereus chloranthus* subsp. *rhyolithensis*, which is currently the only other voucher specimen for this taxon in the SEINet database, is from approximately 140 km ESE of the new record in Sierra County, New Mexico (UNM 25336). The nearest *Echinocereus chloranthus* vouchers to this new record are approximately 20 km NNE in the southwestern corner of Catron County, New Mexico. E. E. Leuck identified these four specimens, collected by P. Pierce in 1967, as *Echinocereus chloranthus* var. *cylindricus* (Engelm.) N.P. Taylor in 1980.

Significance. This is the first vouchered record of *Echinocereus chloranthus* in Arizona, and it confirms previous reports discussed above. It is also the westernmost collection for any of the 14 taxa included in the *Echinocereus viridiflorus* complex, as defined by Blum et al. (2012).

Echinocereus chloranthus is distinguished from other taxa in the *Echinocereus viridiflorus* Engelm. complex mainly by flowers that do not fully open, are not fragrant, and contain substantial orange, brown, and red pigmentation (Taylor 1985). *Echinocereus chloranthus* and its subspecies are also the only taxa in this complex to produce trichomes on the spines (Blum, personal communication). The subspecies of *Echinocereus chloranthus* are distinguished by differing numbers of central and radial spines, as well as differences in habitat and seed structure (Blum and Lange 1998, Blum et al. 2012). *Echinocereus chloranthus* subsp. *rhyolithensis* has more numerous central and radial spines than either *E. chloranthus* subsp. *chloranthus* or *E. chloranthus* subsp. *cylindricus* N.P. Taylor (Blum and Lange 1998, Blum et al. 2012).

Further searches for *Echinocereus chloranthus* subsp. *rhyolithensis* along the border of Arizona and New Mexico, as well as appropriate habitats between the Arizona population and the holotype locality in New Mexico, would provide a more thorough knowledge of the distribution of this taxon. Detailed morphological studies of these and other populations in the *Echinocereus viridiflorus* complex would help continue to elucidate which of the many varieties within this complex are most reasonable in terms of field identification. Until such studies are conducted, it is difficult to assess any potential conservation needs of the cactus.

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NOTEWORTHY COLLECTION

ARIZONA

ROSA STELLATA Wooton subsp. *ABYSSA* A.M. Phillips (ROSACEAE). — Mohave County, Grand Canyon National Park, Cave Canyon (Vulture Canyon), north/northwest-facing section of the canyon, in a roughly 100-meter stretch along the canyon bottom edge extending upwards to base of a cliff face, UTM 12+ 234787E, 3991460N (NAD83) (36.031576°, -113.9434°), with *Atriplex canescens* (Pursh) Nutt., *Bromus rubens* L., *B. tectorum* L., *Ephedra viridis* Coville, *Fallugia paradoxa* (D. Don) Endl. ex Torr., *Ptelea trifoliata* L., and *Rhus aromatica* Aiton var. *trilobata* (Nutt.) A. Gray ex S. Wats., 1,258 m, growing on Kaibab Limestone, about 100 plants present, 25 April 2014, *T. Embrey 170* (GCNP, ARIZ) (NGS Map 2009).

Previous knowledge. Rosa stellata subsp. *abyssa* (Grand Canyon rose) occurs in the Grand Canyon region of northern Arizona. Although first described from Twin Point on the Shivwits Plateau, all other known locations occur to the east of there, including locations from the Little Colorado River Gorge and several locations along the Marble Canyon rim. On the south side of the Grand Canyon, *R. stellata* subsp. *abyssa* is only known from Cataract Canyon, Havasupai Point, and Eremita Mesa; this last locality has not been relocated (Brian 2000, SEINet 2014). Locations from the north rim of the Grand Canyon include the type locality, Fishtail Mesa, 150-Mile Canyon, and several localities along Kanab Canyon.

Significance. Cave Canyon (on the south side of the Colorado River) is the last major canyon in the Grand Canyon and directly adjacent to the Grand Wash Cliffs, which mark the end of the Colorado Plateau and the beginning of the Basin and Range region. The type locality (on the north side) is approximately 58 km to the northeast of this new locality, while the nearest known location on the south side of the river (near the head of Cataract Canyon) is approximately 205 km to the east. *Rosa stellata* subsp. *abyssa* is now known from locations that span the entire Grand Canyon region.

Since *R. stellata* subsp. *abyssa* was described in 1992, several new localities have been discovered, including some of the previously mentioned sites. I examined plants from these new localities to determine the presence or absence of stellately-arranged hairs at the base of the stipitate glands found along the stems, the stipitate glands being, along with the prickly hypanthium, diagnostic for this subspecies (Phillips 1992). The specimens examined, along with their respective localities, include the following: North Rim, overlooking 150-Mile Canyon [stellate hairs absent], *W. C. Hodgson 9821* (ASU0078894); Little Colorado River Gorge vicinity [stellate hairs absent], *D. Roth 1969* (ASU0078895); [stellate hairs absent] *D. Roth 2032* (ASC91662); [stellate hairs present] *D. Roth 2039* (ASC91669); Cataract Canyon (South Rim), [stellate hairs present] *G. Goodwin 1913* (ASC91670); [stellate hairs absent] *G. Goodwin 1551* [ASC86903]; Marble Canyon (eastern Grand Canyon) [stellate hairs present] *B. Hevron 1904* (ASU0078893); Cave Canyon (western Grand Canyon) [stellate hairs absent] *T. Embrey 170* (ARIZ421047).

Although not all extant *Rosa stellata* subsp. *abyssa* specimens were examined, these findings suggest that there is not a geographic correlation for the presence or absence of stellately-arranged pubescent hairs. In the Little Colorado Gorge area, plants collected roughly 2 km apart differed in the presence (*D. Roth 2039*) or absence (*D. Roth 2032*) of stellate hairs. Both Phillips and the current author examined more plants without stellate hairs than with stellate hairs; in his treatment, Phillips (1992) noted that plants from Kanab Creek and Eremita Mesa had less of these stellate hairs than plants from elsewhere in the Grand Canyon. Due to the variability of pubescence in the New Mexico and Texas plants (*Rosa stellata* subsp. *stellata*

Wooton and *Rosa stellata* subsp. *mirifica* (Greene) W. H. Lewis), Phillips did not reduce the plants beyond the one subspecies in Arizona (Phillips 1992). I agree with his conclusion.

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NOTEWORTHY COLLECTION

CALIFORNIA

DITTRICHIA VISCOSA (L.) Greuter (ASTERACEAE). — Solano County, McGary road, 38.198992°, -122.159644°, elev. 43 m., roadside, 5 September 2014, *Zoya Akulova-Barlow* (JEPS). More plants (about 30 total) were found southeast from McGary road, plants reproducing by seeds.

Previous knowledge. Dittrichia viscosa (sticky fleabane) has not been found in California previously. It was collected in the late 1800s as a ballast weed in Florida, New Jersey, and Pennsylvania, but did not become naturalized (Preston 2006).

Significance. This collection is the first report of *Dittrichia viscosa* in California. The species originated from the western Mediterranean region (Ball 1976; Brullo and deMarco 2000) and is potentially invasive; it has become naturalized in Western Australia (Wheeler et al. 2002) and Egypt (Boulos 2002). A closely related species, *Dittrichia graveolens* (L.) Greuter, has become an invasive weed in California (Rosatti 2012, California Invasive Plants Council 2015).

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